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SYSTEMATICS OF THE EUPHORBIACEAE: INTRODUCTION[1]

Grady L. Webster[2]

The first International Conference on the Systematics of the Euphorbiaceae, organized by Michael Huft and Grady Webster, was held at the Missouri Botanical Garden in St. Louis on 14–16 August 1989. Papers were presented by 21 people (several of these with one or more collaborators); of these, 15 authors submitted papers that were accepted for publication and are presented in this issue and the one following.

Although the St. Louis conference was technically the first international symposium on the Euphorbiaceae, it had been preceded by the symposium on Euphorbiales held at the Jodrell Laboratory, Royal Botanic Gardens, Kew, in 1986. However, as can be seen by perusal of the proceedings of that symposium (Jury et al., 1987, Bot. J. Linn. Soc. 94:1–326), the scope of the Kew meetings was different; there was much more emphasis on chemistry and medical applications, and most of the taxonomic contributions dealt with evidence for relationships of the Euphorbiaceae with other angiosperm families.

The St. Louis symposium, in contrast, was "inner-directed," with emphasis primarily on patterns of diversity within the Euphorbiaceae. However, considerable attention was given to questions of relationships with other families in the papers by Vogel et al. on systematics of storage proteins, Kapil and Bhatnagar on comparative embryology, and by Seigler on comparative biochemistry. In fact, one of the interesting aspects of presentations at the symposium was the further elaboration on, and perhaps progress toward resolution of, questions about the "membership" of certain aberrant taxa within the Euphorbiaceae. For example, the studies by Hayden (anatomy), Kapil and Bhatnagar (embryology), and Levin and Simpson (pollen morphology) indicated that controversial genera such as *Antidesma*, *Bischofia*, and *Hymenocardia* are nested within Euphorbiaceae, and recognition of separate families Scepaceae, Bischofiaceae, and Hymenocardiaceae would render the Euphorbiaceae paraphyletic.

A significant part of the symposium contributions was devoted to surveys at the level of subfamily or tribe: Oldfieldioideae (Hayden, Levin & Simpson), Crotonoideae (Nowicke, pollen morphology), Acalyphoideae tribe Plukenetieae (Gillespie, pollen morphology), Euphorbioideae (Mennega, wood anatomy, not published here), Euphorbieae (Gilbert; and Koutnik, not published). At the generic level, there were four studies, on

[1] The International Conference on the Systematics of the Euphorbiaceae was supported by National Science Foundation Grant BSR-8817991. The papers in this issue of the *Annals* and the one following benefitted from the editorial assistance and scientific reviews of Michael J. Huft, Geoffrey A. Levin, and Grady L. Webster.

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Phyllanthus (Haicour et al.), *Jatropha* (Dehgan & Schutzman), *Euphorbia* (Carter), and *Dalechampia* (Armbruster).

These contributions, taken collectively, indicate that there is a significant interest in the Euphorbiaceae at the international level, and that there are a substantial number of workers actively using a variety of methodologies. However, in comparison with symposia on other families such as Compositae, Leguminosae, Solanaceae, and Orchidaceae, it is apparent that the Euphorbiaceae still offer greater stretches of systematically unexplored territory. It is striking that there was no comparative study of DNA or RNA presented at the symposium, and the only detailed molecular analysis was the serological research of Jensen et al. on seed storage proteins. Also notable is the paucity of cladistic analyses of intra- or intergeneric relationships. The paper by Armbruster—with its correlation of pollination relationships, cladistic affinities, and geographic distribution patterns—provided a model for the kind of studies that could be done for many of the taxa in the family.

Despite the regrettable delay in publication of the results of this symposium, we believe that this collection of articles does significantly contribute to the systematics of Euphorbiaceae, both by the presentation of new data and hypotheses, and by the delineation of a research agenda for the future. Both the review of classification and the synopsis of the taxa by Webster summarize what we know at present, and are intended to facilitate their own obsolescence by suggesting some of the profitable directions for research in the future.

CLASSIFICATION OF THE EUPHORBIACEAE[1]

Grady L. Webster[2]

ABSTRACT

The family Euphorbiaceae appears to be monophyletic, despite proposals for segregate families. The Euphorbiaceae display a great variety of growth forms, including at least 17 "models" of Hallé. Anatomical characters particularly useful for classification include wood structure, laticifer type, trichomes, and stomata. Inflorescences are basically dichasial, and pseudanthia have evolved several times. Pollen nuclear number and exine structure provide useful criteria for characterizing genera, tribes, and subfamilies. Structure of the seed coat is characteristic for the family and does not provide evidence for a polyphyletic origin of the family. Pollination is prevailingly entomophilous, and seed dispersal by ants is important in many taxa. Geographic distribution patterns of genera show a concentration of primitive taxa in Africa and Madagascar, although in subfamily Crotonoideae there is evidence of a neotropical center. Disjunctions between Africa and South America are common. Bentham's hypothesis of an Old World origin of the family appears well supported. The basic distribution patterns appear to reflect early (Cretaceous and Paleogene) dispersal across land or narrow water barriers and spectacular but rather trivial instances of long-distance dispersal in the late Tertiary and Pleistocene; Tertiary high-latitude dispersals via the Bering land bridge appear to have been relatively insignificant.

The Euphorbiaceae, although one of the largest dicot families and conspicuous throughout the tropics, have been relatively neglected by systematists in the 20th century. While other families such as Compositae, Leguminosae, and Solanaceae have been the subjects of various symposia, the very first international conference with a major focus on Euphorbiaceae was held at Kew in 1986 (Jury et al., 1987). The Kew symposium, on the Euphorbiales, was heavily biochemical in orientation and focused to a considerable extent on relationships between the Euphorbiaceae and other families. The present symposium in St. Louis is the first in which the classification of the family and its constituent infrafamilial taxa is the major focus of attention.

The history of classification systems for the Euphorbiaceae at the subfamilial and tribal level has been reviewed in the Kew symposium on Euphorbiales (Webster, 1987). In my opinion, the two major milestones in this history were the classifications of Adrien Jussieu (1824), who identified the major series of genera that (after much later revision) correspond roughly to current subfamilies, and Jean Mueller (1866), who provided the first detailed classification of the family into subfamilies, tribes, and subtribes. The originality of Mueller is particularly striking in comparison with the earlier system of Baillon (1858), which was disappointingly uninformative about relationships, and the later ones of Bentham (1880) and Pax (1890), who accepted the general framework of Mueller with relatively minor exceptions. Later revisions by Pax & Hoffmann (1931) and the treatment by Hurusawa (1954) continued to reflect the original ideas of Mueller, despite considerable changes. Although my recent classification (Webster, 1975) appears very different from that of Mueller at first glance, I was struck by how many of the great Swiss systematist's ideas still survive. Even though he went astray in his major subdivisions (based on cotyledon shape) of the "Stenolobeae" and "Platylobeae," Mueller arranged the genera of Euphorbiaceae into subtribes that, in an impressively large number of instances, reflect phylogenetic affinity as presently understood. In reviewing our efforts at this symposium to improve the classification of Euphorbiaceae, it seems evident to me that it is Mueller's foundation we are standing on.

In my classification of 1975, the 300 genera of Euphorbiaceae were grouped into 52 tribes in five subfamilies, with several of the tribes divided into subtribes. The classification presented at this conference shows only a limited number of changes, even though it is quite probable that future research will show that substantial modifications will have to be made. As has often been remarked, the linear arrangement of taxa in a classification is an im-

[1] I wish to thank Robert Rhode for his assistance in preparation of the manuscript and illustrations. Outline maps were provided through the courtesy of Daniel Axelrod.

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perfect way of indicating phylogenetic relationships. Cladistic analysis of the family is badly needed in order to provide a clear idea of the evolution of characters and to test the implicit phylogenetic hypotheses that are lodged in the classification scheme. Unfortunately, the information available for the Euphorbiaceae is imperfect and this, along with the size of the group, makes it difficult to proceed. In my discussion of the family at the Berlin congress in 1987 (unpublished), I provided some informally constructed "family trees" that reflected evolution of characters and used these as the basis for a schematic model of the evolutionary and biogeographic history of the subfamilies and tribes. The present essay is intended to set forth this model in greater detail, in the hope that it will suggest topics for discussion and criticism. In doing so, I emphasize that, while our classification system is a descendant of the system of Jean Mueller in 1866, my scenario for the evolution and biogeography of the Euphorbiaceae is indebted to the perspicacious essay of Bentham (1878), who from extremely imperfect data deduced a model that has proved to be almost clairvoyant in its anticipation of later work on the biogeography of major angiosperm taxa.

Relationships between the Subfamilies

Since the perceptive discussion of Bentham (1878), it has been accepted by later workers (e.g., Pax, 1924), that the subfamily Phyllanthoideae is the primitive group from which other subfamilies are derived. Within the Phyllanthoideae, genera within the tribe Wielandieae, such as *Heywoodia* and *Savia*, appear to represent relicts of the original euphorbiaceous complex that arose probably in the late Cretaceous. These primitive Euphorbiaceae are dioecious shrubs or small trees of seasonal forest habitats in tropical latitudes. They have, as expected, relatively unspecialized flowers with well-developed petals, floral disk, and a pistillode in the staminate flower. The pistillate flower usually has a 3-locular ovary, with two anatropous ovules beneath an obturator. The fruit is a 3-celled capsule, and the seeds have a dry testa, copious endosperm, and a large embryo with a radicle much shorter than the cotyledons. As far as the evidence goes, the chromosome base number is $n = 13$ in these "archaic" taxa of subfamily Phyllanthoideae. Anatomically, the relict Phyllanthoideae have such unspecialized features as vessel elements with scalariform perforation plates, paracytic stomata, and unicellular nonglandular trichomes. Laticifers appear to be absent. If Geranialean families such as Ixonanthaceae are accepted as possible "outgroups," as speculated earlier (Webster, 1967), then it is feasible to compile a list of characters in the Euphorbiaceae for which plesiomorphic (primitive) and apomorphic (advanced) states are defined (Table 1).

An important contribution to identifying significant synapomorphies in subfamily Phyllanthoideae has been made by Levin (1986c) in his cladistic analysis of the subfamily based on foliar characters. Pollen studies on the subfamily, mostly still unpublished (Punt, 1987) or in this symposium (Levin & Simpson, 1994a, b; Nowicke, 1994), show great promise of adding important information for constructing phyletic models. The really major lacuna in our knowledge, for this and other subfamilies, is in biochemical data. Although Hegnauer (1962–1973) and Gibbs (1974) have compiled informative resumes of reports from the biochemical literature, this information is frustrating to the systematist, because it demonstrates a great biochemical diversity in the Euphorbiaceae but at the same time reveals a meager and erratic level of sampling. As a consequence, biochemical data are still of limited usefulness for meaningful comparisons at the tribal and subfamilial levels.

In my 1987 review of the classification of the family, the Euphorbiaceae were implicitly treated as a monophyletic group by the inclusion of such proposed segregate families as Bischofiaceae and Hymenocardiaceae. However, for those interested in relationships within and outside the Euphorbiaceae, it should be noted that this delimitation of the family is not accepted by all of my colleagues. Hymenocardiaceae are accepted as a family by Léonard & Mosango (1985) and by Radcliffe-Smith (1987). Furthermore, Radcliffe-Smith accepts Pandaceae and retains three genera (*Antidesma*, *Bischofia*, and *Uapaca*) only provisionally within the Euphorbiaceae. Jensen (1994) suggests that on the basis of serological data there appear to be two main groups of Euphorbiaceae: Phyllanthoideae + Oldfieldioideae; and Acalyphoideae + Crotonoideae + Euphorbioideae. This binary arrangement of "biovulate" and "uniovulate" taxa parallels the arrangement proposed by Mahlberg (1987) on the basis of laticifer morphology. On a phenetic basis, this basic dichotomy appears intuitively reasonable, but it remains to be seen whether it will be substantiated by critical phylogenetic studies.

Meeuse (1990) went much further and proposed recognizing nine families, with Euphorbiaceae being restricted mainly to the "uniovulate" subfamilies Acalyphoideae, Crotonoideae, and Euphorbioideae. There is not sufficient space here to analyze

TABLE 1. List of primitive (plesiomorphic) and derived (apomorphic) characters in the Euphorbiaceae.

Character	Primitive state	Derived state
1. Habit	Trees/shrubs	Herbs/vines
2. Branching	Monopodial	Sympodial
3. Phyllotaxy	Alternate	Opposite
4. Leaf shape	Simple	Lobed; compound
5. Leaf venation	Pinnate	Palmate
6. Stipules	Present	Absent
7. Vessel perforation	Scalariform	Simple
8. Vascular rays	Multiseriate	Uniseriate
9. Internal phloem	Absent	Present
10. Laticifers	Absent	Present
11. Trichomes	Simple	Stellate; lepidote
12. Foliar glands	Absent	Present
13. Inflorescence	Axillary	Terminal
14. Calyx aestivation	Imbricate	Valvate; reduplicate
15. Petals	Present; free	Absent; connate
16. Disk	Present	Absent
17. Stamen number	5–10	1–4; over 10
18. Filaments	Free	Connate
19. Anther dehiscence	Longitudinal (vertical)	Horizontal
20. Pollen nuclei	2-nucleate	3-nucleate
21. Pollen exine	Semitectate	Tectate; intectate
22. Pollen apertures	Colpi	Pores; inaperturate
23. Aperture number	3	4 or more
24. Pistillode	Present	Absent
25. Carpel number	3–5	1–2; 6 or more
26. Style branches	Bifid	Unlobed; multifid
27. Style union	Free	Connate
28. Ovule number	2/locule	1/locule
29. Ovule configuration	Anatropous	Hemitropous
30. Embryo sac	Monosporic	Disporic; tetrasporic
31. Fruit	Dehiscent	Indehiscent
32. Seeds	Ecarunculate	Carunculate
33. Seed testa	Dry	Fleshy
34. Endosperm	Present	Scanty or absent
35. Cotyledon/radicle length	2+	Less than 2
36. Cotyledon/radicle width	2+	Less than 2

his provocative arguments, but I believe that he has overemphasized the seed-coat data of Corner (1976) and that the case for fragmentation of the family remains unpersuasive. Clearly, though, the monophyly of the Euphorbiaceae as a whole, and of the individual subfamilies, needs to be more convincingly demonstrated in the course of any detailed analysis of the infrafamilial taxa.

REVIEW OF SYSTEMATIC CRITERIA

At present, the overwhelming preponderance of the data available for interpreting the patterns of phylogeny within the Euphorbiaceae comes from gross vegetative and floral morphological characters that have been used as diagnostic taxonomic features. In evaluating relationships within individual tribes or subfamilies, particular morphological characters have proven to be especially useful. So far only pollen morphology has provided micromorphological characters that are useful in determining systematic affinities in all five subfamilies, as shown by the works of Erdtman (1952) and Punt (1962, 1987). However, the studies of Levin (1986a, b, c) demonstrate that foliar venation provides systematically valuable characters in subfamily Phyllanthoideae, and this may prove to be true for other characters as well. The survey of chromosome numbers by Hans (1973) indicates that these may well yield clues to defining lines of systematic affinity, but at present the available data are frustratingly incomplete. Biochemical data from comparative studies of secondary compounds such as alkaloids and terpenes can hardly fail to produce

results of great interest, especially at the tribal and generic levels, but at present we have only tantalizing scraps of data from scarcely more than a handful of genera.

In all of the classifications of the Euphorbiaceae proposed before 1975, the major criteria were drawn from details of gross morphology observable with the naked eye or a dissecting lens. Even after demonstrating the systematic importance of pollen characters by Erdtman (1952), the systems of Hurusawa (1954), Hutchinson (1969), and Airy Shaw (1972, 1975) still depended almost entirely on the same data sets available to Baillon, Mueller, Bentham, and Pax. In order to expedite future work on classification of the family, it seems appropriate in this essay to review the characters that show promise in interpreting evolutionary trends and lines of affinity. Ecological characters are not discussed, except for those relating to pollination and dispersal with a possibly significant effect on the evolution of reproductive structures.

A. GROWTH FORM

The Euphorbiaceae display an extraordinary range of growth forms, perhaps equaling or surpassing any other angiosperm family (Hallé, 1971). Trees and shrubs predominate, as one would expect of a primarily tropical family, but herbs have evolved independently in all five subfamilies. The greatest diversity of growth form is seen in the genera *Phyllanthus* (Webster, 1956) and *Euphorbia* (Croizat, 1972; Cremers, 1977), which show a wide range of adaptations to relatively mesic and xeric habitats, respectively.

In recent years the architecture of tropical trees has been studied on a comparative basis, so that for the first time the bewildering diversity of form in tropical taxa can be comprehended through the scheme of about two dozen basic models proposed by Hallé and coworkers (Hallé & Oldeman, 1970; Hallé et al., 1978). Determination of the membership of a particular taxon in the Hallé/Oldeman model system is difficult and sometimes impossible from examination of herbarium specimens; observations of the germination and ramification of seedlings or saplings may be required. Despite the considerable number of Euphorbiaceae that have been studied, the sampling of taxa in the subfamilies and tribes is still incomplete. However, further studies may provide important insights into the phylogeny of suprageneric taxa.

At the present time, no less than 17 models have been reported for the woody Euphorbiaceae; and a significant number of herbaceous, scandent, and succulent Euphorbiaceae show additional variations that cannot be easily assigned to any of the Hallé models. All of the subfamilies except for the Oldfieldioideae show more or less comparable diversity, and there appear to be differences between some of the subfamilies that may be phylogenetically significant.

In subfamily Phyllanthoideae branching patterns tend to be monopodial and inflorescences axillary; the prevalent unspecialized patterns are those shown by the models of Attims, Aubreville, and Rauh. A striking tendency is that toward monopodial plagiotropic branching (Roux's model) as in *Flueggea*, *Phyllanthus* (input), and *Drypetes*. A further specialization of this pattern yields the deciduous, floriferous phyllomorphic branchlets (Cook's model) found in several genera of tribe Phyllantheae subtribe Flueggeinae, including *Breynia*, *Glochidion*, *Phyllanthus*, and *Sauropus*. This highly specialized growth form, first documented by Dingler (1885) and designated as "phyllanthoid branching" by Webster (1956), has been thoroughly analyzed by Roux (1968), Bancilhon (1971), and Rossignol & Rossignol (1985).

The subfamily Oldfieldioideae resembles the Phyllanthoideae in having relatively unspecialized monopodial branching patterns that agree with the models of Attims and Rauh. However, *Stachystemon polyandrus* (F. Muell.) Benth., and perhaps a few other taxa, appear to fit the model of Koriba, in which extension of the main axis is interrupted by a terminal inflorescence, leading to sympodial growth. In the three uniovulate subfamilies, determinate/sympodial growth patterns predominate. Among the Acalyphoideae studied, about half (20 genera) show the unspecialized patterns of Attims and Rauh, but a number of genera follow the models of Koriba and Leeuwenberg, in which the main axis is terminated by an inflorescence and branching is more or less dichasial in nature. In the Crotonoideae, the model of Koriba seems to be the most common, and that of Rauh is about as prevalent as that of Attims. Finally, in the Euphorbioideae, which are possibly the latest subfamily to evolve, the branching patterns are more specialized. Only six out of 32 genera show the patterns of Attims and Rauh, as compared to 15 for the models of Koriba and Leeuwenberg. Furthermore, the models of Prévost and Nozeran, almost or entirely absent in the other subfamilies, are well represented with nine genera. Even though these figures are influenced by the large number of models found in *Euphorbia*, the divergence of the subfamily Euphorbioideae in growth pattern is clear.

The vegetative and reproductive morphology of

Euphorbia has received a great deal of attention, and a striking sequence of modifications of growth form can be traced within the tribe Euphorbieae. It is particularly notable that the branching pattern of *Anthostema* is referred to the model of Nozeran by Hallé & Oldeman (1970); the ramification in that genus recapitulates the origin of the cyathium from a concrescent verticel of floriferous branches, with the abortive axis surmounted by a pistillate flower. Nozeran (1953) had appropriately applied the term "pre-cyathium" to the bisexual spikes of Hippomaneae such as *Sapium* or *Stillingia*. A whorl of four or five of these "spikes" (which are really thyrses) produced on a plant growing according to the model of Nozeran could indeed have given rise to the primitive cyathium, although there are still problems—in the absence of any living "missing link"—in specifying how the lateral and basal flower in the Hippomanean thyrse becomes the terminal flower in the cyathium (see Gilbert, 1994).

One can argue that the ultimate point in vegetative evolution in the Euphorbiaceae is attained in *Chamaesyce*, where the seedling axis is usually abortive above the cotyledons and the axial portion of the plant is virtually all sympodial. In the abortion of the main axis, the pattern suggests the model of Nozeran, but the subsequent dichasial pattern is a two-dimensional plagiotropic variant of the model of Leeuwenberg. Hurusawa (1954) has claimed that the conformation of axes in *Chamaesyce* represents the terminus of a reduction series beginning in *Euphorbia* subgenus *Esula* and progressing through subgenus *Agaloma* by retardation of the main axis relative to the lateral anthocladia. However, in a recent study, Hayden (1988) showed that the lateral branches in *Chamaesyce* arise at the cotyledonary nodes, and that the apparent homology with the terminal pleiochasial whorl in *Euphorbia* is doubtful.

The adaptive significance of the growth forms in the Euphorbiaceae is not as clear as their utility as systematic characters (a common situation in many angiosperm taxa). Part of the difficulty is that the changes in some ramification patterns are due to simple shifts in relative rates of meristematic activity, so that reversals of trends and convergences appear common indeed. A striking instance of this, for example, is shown by the distribution of Troll's model in the Euphorbiaceae: in the Phyllanthoideae, it is found in woody taxa of *Briedelia* and herbaceous *Phyllanthus*, where it appears derived from Attims's model; but in the Euphorbioideae, it seems to have evolved in *Pedilanthus* via Attims's model and in *Actinostemon* via Prévost's model. Cremers (1977) demonstrated 10 different models in Madagascan *Euphorbia*, and there appear to be some species that do not fit any model. Even worse, species such as *Euphorbia stenoclada* Baillon and *E. abyssinica* Gmel., which conform to the models of Attims and Rauh, have surely been derived from ancestral taxa with the more "specialized" models of Prévost and Nozeran.

It is understandable that correlations between architectural models and ecological conditions are imperfect and often obscure, in view of the fact that the vegetative growth patterns interact with reproductive adaptations in a complicated fashion. Certain models, such as Cook's and Nozeran's, clearly predominate in rainforest habitats; but others, such as Attims's, are found in both rainforests and deserts. Evidently the Euphorbiaceae have entered such a wide variety of habitats during their radiation that no simple correlations can be expected. Nevertheless, the coevolution of branching patterns and reproductive structures in some taxa of Euphorbiaceae is sufficiently striking that more attention needs to be given to field observation of the architectural models.

B. ANATOMY

Anatomical characters have been regarded as important in the classification of the Euphorbiaceae since the essay of Pax (1884), which first established the importance of laticifers as a character for defining natural groups. Pax used laticifer type (articulated vs. nonarticulated), phloem characters, and trichome type as the major anatomical characters to support his redivision of the major suprageneric taxa. These studies were considerably extended in the following decade by Radlkofer and his students. Radlkofer (1870) emphasized anatomical characters in a paper establishing the new euphorbiaceous genus *Pausandra*; and a series of his students surveyed most of the family anatomically (Rittershausen, 1892; Froembling, 1896; Rothdauscher, 1896; Herbert, 1897). The first really critical anatomical survey of the family was provided by Solereder (1899), who reviewed the contributions of Radlkofer's group and added many observations of his own. Gaucher (1902) published an independent anatomical survey of the family that curiously omits all mention of the works of the German school. He was criticized for this by Solereder (1908), who also pointed out mistakes in his observations. However, Gaucher's study did have the merit of providing a comparative review of anatomical characters arranged by tribe.

Anatomical studies of wood by Pax and others,

up to the turn of the century, seem mainly to have been made on twig material. The first important contribution based on studies of mature wood from tree trunks appears to be that of Janssonius (1929, 1930), based largely on Indonesian taxa. Janssonius pointed out the divergent wood structure of *Daphniphyllum* as an indication of its lack of relationship to the Euphorbiaceae. The most interesting of his findings was his designation of a group of genera of subfamily Phyllanthoideae (*Aporosa*, *Baccaurea*, *Drypetes*, and *Putranjiva*) as characterized by thick-walled nonseptate fibers, abundant metatracheal parenchyma, and scalariform vessel perforations. Bamber (1974) amplified the work on fiber morphology by showing that thick-walled fibers ("type II") also occur in genera of subfamily Oldfieldioideae (*Dissiliaria* and *Petalostigma*). Mennega (1987) expanded the survey and showed the presence of type II fibers in a number of additional genera of Phyllanthoideae and Oldfieldioideae. Hayden (1980) reviewed the wood anatomy of subfamily Oldfieldioideae as part of a comprehensive anatomical survey.

Metcalfe & Chalk (1950), in the most recent comprehensive anatomical review of the entire family, created some anatomical groups that partly correspond to accepted subfamilial and tribal concepts but in a number of respects are contradictory. Their "Group A" of the Phyllanthoideae includes the genera with the syndrome of characters first identified by Janssonius: thick-walled (Bamber "type II") fibers, abundant parenchyma, and scalariform vessel perforations. It appears that "Group A" taxa such as tribes Wielandieae and Antidesmeae may indeed have the most anatomically primitive characters in the Euphorbiaceae. However, there are also some outstanding discrepancies between the arrangement of Metcalfe & Chalk and the classification accepted currently. The most notable is the position of *Acalypha*, which is grouped by them (and Janssonius) with the Phyllanthoideae; but this disposition is contradicted by so much other evidence that the resemblances of *Acalypha* to the Phyllanthoideae must be due entirely to convergence. The studies of Mennega (1987) on wood anatomy in the Phyllanthoideae in general supported the relationships in the classification of Webster (1975), although some discrepancies remain.

Although Pax (1884) placed great emphasis on laticifer type in defining the major infrafamilial subdivisions, the use of laticifers to address problems at higher ranks was subsequently neglected despite the plea by Solereder (1908) for new developmental and comparative studies of laticifers. Dehgan & Craig (1978) reported a variety of laticifers in the single genus *Jatropha*: single-celled idioblasts, coenocytic laticifers without cross-walls, and classic "articulated" laticifers. Their results in some respects contradict the findings of Rao & Malaviya (1964). Mahlberg (1975, Mahlberg et al., 1987), in a series of studies showed the systematic importance of laticifers in *Euphorbia*, particularly with respect to the type of starch grains produced. Only recently, however, has Rudall (1987) provided the first modern survey of laticifer types within the family and amply demonstrated the importance of laticifers in evaluating relationships. Rudall's survey indicates that articulated laticifers are confined to subfamily Crotonoideae and nonarticulated ones to the Crotonoideae and Euphorbioideae, except for a few reports (needing confirmation) of nonarticulated laticifers in the Acalyphoideae. Mahlberg et al. (1987) interpreted this laticifer data radically by proposing a subdivision of the Euphorbiaceae into three families based on the groups Phyllanthoideae, Acalyphineae, and Hippomanoineae of Pax (1884). Clearly there is still an urgent need for more intensive sampling of tribes in the uniovulate Euphorbiaceae for morphological and anatomical data.

Another important source of systematic data is furnished by trichomes. Mueller (1866) was the first to emphasize trichomes as a major character in his revision of the family. Froembling (1896) reviewed the trichome types in the Crotonoideae, which show the greatest diversity among the subfamilies. The subsequent neglect of trichome characters in the Euphorbiaceae is indicated by the fact that the last detailed systematic review is that of Solereder (1899). Inamdar & Gangadhara (1977) presented a survey of euphorbiaceous trichomes, but their sample of only 53 species was too limited to be systematically meaningful. A more comprehensive sample of 250 species by Rao & Raju (1985) provided a succinct review of the systematic distribution of trichome types. Most of the trichome variation of systematic interest is found in subfamilies Acalyphoideae and Crotonoideae, where various kinds of malpighiaceous, stellate, and lepidote types occur; in the other three subfamilies simple unicellular or multicellular hairs overwhelmingly predominate.

The most unusual trichomes found in the Euphorbiaceae are stinging hairs, which have evolved independently in the Acalyphoideae and Crotonoideae. The hairs in *Cnidoscolus* (Crotonoideae–Manihoteae) are of the common *Urtica* type, with a deciduous bulbous tip (Thurston & Lersten, 1969). Breckon (1975) has described considerable variation in morphology of the stinging hairs in Mex-

ican species of *Cnidoscolus*. Within the Acalyphoideae, stinging hairs of a fundamentally different type are known from the tribe Plukenetieae. These were carefully described by Knoll (1905) as composed of a central crystaliferous cell of subepidermal origin surrounded by a jacket of three epidermal cells; Knoll's interpretation of these trichomes has been confirmed by the ultrastructural studies of Thurston (1976). The common possession of this unique type of trichome (along with other characters such as columnar compound styles) provides a powerful argument for assigning *Dalechampia*, which has been previously kept in a separate tribe, to the Plukenetieae.

The Euphorbiaceae are also impressively rich in foliar glands, which appear to have arisen de novo within the family, as they are absent in the Wielandieae and other apparently archaic taxa in the Phyllanthoideae. In both the Phyllanthoideae and Oldfieldioideae, foliar glands are restricted in occurrence, but they are very common in the uniovulate subfamilies. Diffuse pellucid-punctate glands have been reported in the unrelated genera *Clutia* (Acalyphoideae) and *Suregada* (Crotonoideae). Discrete embedded laminar glands are widespread, occurring in many Acalyphoideae (e.g., in Acalypheae, Alchorneae, Bernardieae, Chrozophoreae, Omphaleae, and Plukenetieae). In the Crotonoideae, glands most often occur at the junction of lamina and petiole (e.g., in Crotoneae, Manihoteae, Micrandreae). In *Jatropha* (Dehgan & Webster, 1979), and many other Crotonoideae and Acalyphoideae, glands are very diverse; glands on leaf margins often appear to intergrade with petiolar glands.

Bernhard (1966), in a survey of the morphology and anatomy of euphorbiaceous foliar glands, has suggested that the marginal glandular teeth in many Euphorbiaceae may be of a separate origin from the laminar or petiolar glands. Belin-Depoux & Clair-Maczulajtys (1974, 1975) elucidated the anatomical structure of petiolar glands of *Aleurites* with light microscopy and TEM, and Belin-Depoux (1977) showed that the foliar glands of *Alchornea cordata* Benth. (Acalyphoideae) are fundamentally similar to those of *Aleurites* (Crotonoideae).

Stomatal development within the Euphorbiaceae shows considerable variation, as indicated by Raju & Rao (1977). They found an overwhelming predominance of paracytic stomata in the woody taxa of most of the 17 tribes sampled, with anisocytic stomata becoming prominent mainly in herbaceous Phyllanthoideae (as indicated earlier for *Phyllanthus* by Webster, 1956). The most aberrant situation reported by Raju & Rao is the high percentage of anomocytic stomata in *Chamaesyce* (Raju & Rao, 1987). Not unexpectedly, Kakkar & Paliwal (1974) found a considerable diversity of stomatal types in *Euphorbia*. Dehgan (1980) found that the two subgenera of *Jatropha* can be distinguished by stomatal type and also surface of hairs (smooth versus verruculose).

Foliar venation, a neglected character, has only recently been used by Levin (1986a, b, c) to provide new insights into relationships within subfamily Phyllanthoideae. Similar studies on the other subfamilies would no doubt be illuminating. So far, almost all of the work in other subfamilies has been done on tribe Euphorbieae (Sehgal & Paliwal, 1974). The characteristic jacketed venation in *Chamaesyce* has attracted interest because of its correlation with C_4 photosynthesis (Webster et al., 1975).

Although the vast majority of Phyllanthoideae and Euphorbioideae have simple entire leaves, the Acalyphoideae and Crotonoideae have predominately toothed or lobed leaves. Hickey & Wolfe (1975) have designated the Euphorbiaceae as having a "Dilleniid" leaf type on the basis of actinodromous venation and "Violoid" marginal teeth, in which the medial vein expands into a glandular termination without a deciduous apical seta. However, in the most primitive Phyllanthoideae the leaves are entire and camptodromous, so the "Violoid" teeth would appear to have arisen de novo within the family. Furthermore, the foliar teeth in Euphorbiaceae are variable; for example, deciduous setae occur in the Hippomaneae, which would make them "Theoid" instead of "Violoid." A survey of foliar venation and tooth types in the Acalyphoideae and Crotonoideae will be necessary to verify the claim by Hickey & Wolfe that the leaves of Euphorbiaceae betray a "Dilleniid" instead of "Rosid" affinity.

Vascular anatomy of petioles has been studied from cross sections by Dehay (1935), who showed considerable variation in stelar configurations. However, Dehay did not attempt to untangle variation correlated with leaf size from that due to systematic affinity, and it seems unlikely that this character will prove to be of general utility. However, on a more restricted level, Miller & Webster (1962) used differences in petiolar steles to separate *Cnidoscolus* from *Jatropha*, and Dehgan (1982) found that different degrees of petiolar stelar dissection were significant at the sectional and subsectional level in *Jatropha*.

A significant foliar structure in many Euphorbiaceae are the stipules inserted at the base of the petiole (Uhlarz, 1978). In many of the Phyllan-

thoideae and occasional genera (e.g., *Manihot*) elsewhere, the stipules are early deciduous (caducous), even if they are rather large. Phyllanthoid stipules are entire, but in the Acalyphoideae and Crotonoideae they can become lobed, dissected, or glandular. In a considerable number of taxa, stipules have become reduced or even entirely suppressed. Sometimes one or a few species in a genus (e.g., *Hyeronima alchorneoides* F. Allemão) have stipules, whereas they are absent in related species. Many species of *Croton* lack stipules, whereas they are large and conspicuous in others. Most notably, in *Euphorbia* presence or absence of stipules is a diagnostic character for some sections and subgenera. Although stipules presumably play some adaptive role in protecting stem apices and leaf primordia, no convincing explanation has been given for their presence or absence in closely related taxa.

C. INFLORESCENCES AND FLOWERS

Since Euphorbiaceae have unisexual flowers that are often reduced, grouping of flowers into inflorescences is often important for pollination, and inflorescence structure is an important systematic character in many instances. Monoecious and dioecious flower production are widespread, with monoecious perhaps somewhat more common. It seems likely that dioecy is primitive in the family, judging from sexual dispositions in "basal" taxa (e.g., Wielandieae) in the subfamily Phyllanthoideae. However, this seems to have been readily reversible, since monoecious taxa appear to have given rise to dioecious ones in *Croton*, *Euphorbia*, *Phyllanthus*, and other genera. Inflorescences as a whole are proterogynous, although within some genera (e.g., *Euphorbia*) transitions can be found from proterogyny to proterandry. Pollination of Euphorbiaceae is mainly entomophilous, but wind pollination has evolved independently in all of the subfamilies (except in the Euphorbioideae, where anemophily may be absent): *Hymenocardia* (Phyllanthoideae); *Picrodendron* (Oldfieldioideae); *Acalypha* and a considerable number of other genera (Acalyphoideae); and *Borneodendron* and *Eremocarpus* (Crotonoideae). Wind-pollinated taxa usually have spicate inflorescences, but so do many entomophilous taxa.

It seems apparent that inflorescence structure in the Euphorbiaceae is fundamentally dichasial. This is most strikingly evident in genera of Crotonoideae such as *Cnidoscolus* and *Jatropha*, which have elaborate compound dichasia. However, in the Phyllanthoideae, it can usually be seen that the flowers in axillary clusters are produced cymosely. The thyrse, often mistakenly described as a spike, is very common in all five subfamilies. In subfamily Euphorbioideae there is a striking reduction series from the diffuse "paniculate" inflorescences of *Senefeldera* through the thyrses of Hippomaneae such as *Sapium* or *Stillingia* to the pseudanthia (cyathia) of the Euphorbieae. Examples of pseudanthia or "subpseudanthia" can be found in isolated genera in most of the subfamilies: Phyllanthoideae (*Uapaca*), Oldfieldioideae (*Pseudanthus*), Acalyphoideae (*Dalechampia*, *Pera*), and Euphorbioideae (tribe Euphorbieae). In the tribe Euphorbieae there has been the greatest "radiation" of pseudanthial structure, with several cyathial genera apparently evolved from a common ancestor.

Floral form in the Euphorbiaceae shows tremendous diversity, partly as a consequence of independent evolution of staminate and pistillate flowers and partly as the result of adaptation to a variety of vectors (wind, bees, flies, butterflies, birds, and mammals). A masterly illustrated survey of floral gross morphology, with emphasis on ontogeny, was made by Baillon (1858), the most perceptive morphologist of the 19th-century specialists on the family. Since Baillon's work there has been only one other comprehensive survey, that of Michaelis (1924). However, Venkata Rao more recently (1971, 1972) studied vascular anatomy of a considerable number of genera and attempted to relate his findings to the phylogeny of the family. Unfortunately, he sometimes generalized excessively from single instances, as when he suggested that the flowers of *Jatropha* are the most primitive in the family because they are often hermaphroditic; this is contradicted by the specialized pollen grains and secretory apparatus in that genus.

Venkata Rao pointed out a number of trends in floral morphology within the Euphorbiaceae, the most obvious being that of reduction in size and number of parts. Reduction is sometimes correlated with shift to wind pollination, as in tribe Acalypheae; but in other instances (Phyllantheae, Euphorbieae) it clearly is not. As noted by Venkata Rao, there are also trends to increase the number of floral parts; here again, there is no correlation with anemophily, since the highest numbers of stamens, for example, occur in *Croton* (entomophilous) and *Ricinus* (anemophilous). A particularly evident reduction tendency is loss of the corolla, which is so prevalent that Euphorbiaceae are often placed in "apetalous" groups. This affects both sexes but is most striking for the pistillate flowers; petaliferous staminate flowers and apetalous pistil-

late flowers occur in most species of *Croton* and in other Crotonoideae, as well as many Acalyphoideae (e.g., Agrostistachydeae, Chrozophoreae). Two subfamilies, Oldfieldioideae (except *Croizatia*) and Euphorbioideae, are apetalous in both sexes. In the presumably wind-pollinated oldfieldioid genera *Androstachys* and *Stachyandra*, the staminate flowers have a chaotic organization of tepals and stamens that led Leroy (1976) to propose a curious theory suggesting that the staminate flowers in these genera are modified inflorescences.

The calyx in Euphorbiaceae varies greatly in configuration and number of parts. Where the corolla is absent, petaloid calyces may occur, as in *Cnidoscolus* and *Manihot*. Croizat (1943) suggested that the perianth of *Cnidoscolus* is corolline and that the calyx had been lost; however, the evidence from vascular traces in *Manihot* contradicts this idea (Venkata Rao & Ramalakshmi, 1968; Venkata Rao, 1971). In past systems of classification of the Euphorbiaceae, great stress has been placed on aestivation of the calyx (whether imbricate or valvate), a practice initiated by Mueller (1866). Although Baillon (1873) rightly objected to the excessive weight accorded the character by Mueller, it was still extensively used by Pax (1890) and Pax & Hoffmann (1931). Comparison of the aestivation character with evidence from other characters (wood anatomy, trichomes, and pollen) strongly suggests that it must be used with caution.

The euphorbiaceous corolla, where present, is variable in size and color; large showy red or white flowers occur mainly in the Crotonoideae (e.g., in *Aleurites*, *Jatropha*). The petals are usually distinct, but may be coherent or connate in some Crotonoideae such as *Jatropha* (Dehgan & Webster, 1979) and some Aleuritideae (Léonard, 1962). Venkata Rao & Ramalakshmi (1968) reported that vascularization of petals (with three bundles) is usually similar to that of the sepals, although it may be obsolete in the reduced petals of *Codiaeum* and *Croton*.

The floral disk (nectary) is a conspicuous feature of many euphorbiaceous flowers. Baillon (1858) regarded it as receptacular in nature and was followed in this interpretation by most later workers (e.g., Bentham, 1880; Pax & Hoffmann, 1931). On the other hand, Michaelis (1924) proposed that the disk is of staminodial origin, partly because of the apparent obdiplostemony in flowers of taxa such as *Jatropha*, and partly because of the staminodelike appearance of disk-segments in various genera such as *Chiropetalum*, *Clutia*, and *Poranthera*. However, Venkata Rao & Ramalakshmi (1968) have shown that the vascularization of the disk is highly variable; and Webster (1956) found that in *Phyllanthus* the degree of vascularization seems to be correlated with mass; small disk-segments are usually nonvascularized. The preponderance of evidence seems to be against the view of Michaelis and in favor of the classical concept of Eichler (1875) that the floral disk is of receptacular nature and not an independent whorl of the flower.

The euphorbiaceous androecium displays a protean diversity that has provided many characters used by Mueller (1866) and later workers to diagnose subtribes, genera, and infrageneric taxa. Michaelis (1924) hypothesized that the primitive condition in the family was an androecium of an indefinite number of stamens in many whorls. Venkato Rao & Ramalakshmi (1968), in contrast, suggested that the primitive condition is 10 stamens in two whorls, as in *Jatropha*. However, on the basis of the prevalent condition in the Wielandieae and associated tribes of the Phyllanthoideae, I think that an androecium of a single whorl of five or six stamens is most likely to be ancestral within the family. Mueller (1866), in defining subtribes, placed great emphasis on the insertion of the stamens; in practice, this usually depended on whether they were inserted around a pistillode or disk. However, in some groups such as the Drypeteae it is difficult to distinguish a pistillode from a confluent central disk; and in Crotonoideae such as *Cnidoscolus* or *Jatropha*, it is not easy to tell whether the slender projections at the top of the staminal column represent staminodes or a pistillode.

Mueller was sharply criticized by Baillon (1873) for placing undue emphasis on anther form and dehiscence as generic characters. Because of transitional situations, distinctions between extrorse and introrse dehiscence are sometimes difficult to verify. There are all degrees of shift of the plane of anther dehiscence, not only between extrorse and introrse but between basifixed/versatile and longitudinal/horizontal. The most bizarre specializations are found in the Acalypheae (subtribe Lasiococcinae), where the filaments of the stamens are united into branching fascicles and the number of anthers proliferated, reaching the extreme degree of elaboration in *Ricinus*. Although there has been much profitless spilling of ink in speculations about the androecium of *Ricinus*, it tells us nothing about the role of telomes in the angiosperm flower, as pointed out by van der Pijl (1952). Venkata Rao & Ramalakshmi (1968) made the fantastic suggestion that the branched stamen complex of *Ricinus* is primitive and that conventional dithecous

anthers are derived by reduction; abnormal supernumerarily lobed anthers in *Jatropha curcas* L. are supposed to represent an intermediate condition. In fact, the derivation of the androecium of *Ricinus* is clearly suggested by comparison with the related genus *Adriana*, which has a large number of completely separate stamens. Although more careful morphological study is needed, it appears that Airy Shaw (1980) may have been correct in suggesting that the fascicled stamens in *Homonoia* and *Lasiococcus* were derived independently from those in *Ricinus*.

Pollen grains of the Euphorbiaceae are produced in tetrads by simultaneous cytokinesis, as in most dicots (Davis, 1966), and are always monads at maturity. At anthesis the pollen grains may be either binucleate or trinucleate. Webster & Rupert (1973) showed that the nuclear condition of pollen is a significant taxonomic character in defining major phyletic lines in the family: the Phyllanthoideae, Oldfieldioideae, and Acalyphoideae appear to be entirely binucleate, while in the Crotonoideae and Euphorbioideae both binucleate and trinucleate pollen occur. In a study of the tribe Euphorbieae, Webster, Rupert & Koutnik (1982) showed that trinucleate pollen originated several times and that the distribution of pollen nuclear number is an important criterion in defining subgenera and sections. These observations support the "Schürhoff-Brewbaker Law," which postulates that the shift from binucleate to trinucleate pollen is irreversible.

The morphology of pollen grains in Euphorbiaceae is so diverse that only the Acanthaceae can rival it. Although Mueller (1874) illustrated a considerable number of pollen grains of Brazilian Euphorbiaceae, he made no use of pollen morphology in defining taxa at any level. Pax (1884) dismissed the systematic utility of pollen despite the paper by Radlkofer (1870) emphasizing the pollen characters of *Pausandra*. We owe to Erdtman (1952) the first convincing demonstration that pollen morphology offers decisive clues to systematic relationships within the Euphorbiaceae. Erdtman's suggestion that genera with crotonoid sexine patterns should be associated irrespective of their positions in the system of Pax & Hoffmann (1931) has been supported by Punt (1962) and later workers. Köhler (1965), on the basis of a survey of pollen of the biovulate taxa, was able to make a persuasive argument for recognizing a new subfamily, the Oldfieldioideae. The reclassification of subfamilies and tribes by Webster (1975) was strongly influenced by these light microscopic studies and by unpublished SEM observations (Webster et al., unpublished). The importance of palynological characters is further highlighted by the studies in this issue on Oldfieldioideae, Crotonoideae, and tribe Plukenetieae.

The great pollen diversity in Euphorbiaceae makes it difficult to identify consistent trends. As one might expect, taxa that are presumed to be wind-pollinated share a tendency toward reduction of colpi and sexinous ornamentation, e.g., in *Hymenocardia* (Phyllanthoideae), *Longetia* (Oldfieldioideae), *Acalypha* (Acalyphoideae), and *Borneodendron* (Crotonoideae). However, *Ricinus* is a partial exception; although the sexinous ornamentation is reduced, the grains have very prominent colpi. Within all of the subfamilies except the Euphorbioideae, there is a tendency for multiplication and shortening of apertures that leads to polyporate grains; in the Crotonoideae, the apertures become obsolete. Crotonoid sexinous ornamentation is a unique synapomorphy within subfamily Crotonoideae. Transmission electron micrography will no doubt provide even more valuable insight into tribal relationships within the subfamilies.

The gynoecium in Euphorbiaceae is almost as diversely modified as the androecium. Although the carpel number is three in the majority of taxa, it is reduced to two in a number of genera and to one in several, including *Antidesma* (in part), *Crotonopsis*, *Drypetes* (in part), and *Jatropha*. On the other hand, it is increased to six or more in species of a number of genera, including *Glochidion*, *Hippomane*, *Hura*, and *Phyllanthus*. It is not even certain that 3-carpellate gynoecia represent the plesiomorphic condition in Euphorbiaceae, since within the Wielandieae there are genera characterized by four carpels (*Heywoodia*) and five (*Wielandia*). In *Margaritaria* carpel number fluctuates between two and six, and varies from three to six in the single species *M. nobilis* L.f. (Webster, 1979).

Stylar variation is marked and has been used often for specific, generic, and even tribal diagnoses. In the majority of genera the styles are elongated and bifid (often so deeply as to be bipartite); in scattered genera and in the subfamily Euphorbioideae, they are undivided in most genera (but usually bifid in *Euphorbia*). On the other hand, the two style branches may be further subdivided so that each style may have four or eight stigmas, or even more; this is particularly common in *Croton*. Usually the styles are connate, if at all, only at the base, but in the tribe Plukenetieae they are often connate to the tip into a long stylar column which may be modified in bizarre shapes. Finally, in a number of genera (e.g., *Endospermum*, *Glo-*

chidion, Tetrorchidium) the styles are reduced to sessile, often petaloid, stigmas. Rather unexpectedly, stylar morphology is not clearly correlated with pollination vectors: anemophilous taxa may have either highly dissected styles (*Acalypha*) or undivided entire styles (*Alchornea*).

Ovular characters have been regarded as significant within the Euphorbiaceae since A. Jussieu (1824) originally established the distinction between biovulate and uniovulate taxa as a diagnostic criterion. There is no evidence of reversion from the presumed derived condition, uniovulate, to the biovulate condition. However, it remains unclear whether the transition from gynoecia with biovulate locules to gynoecia with uniovulate locules occurred only once. In other words, we cannot yet be certain that the uniovulate taxa, treated by Pax (1890) as subfamily Crotonoideae, represent a monophyletic group.

As pointed out by Baillon (1858), ovules of Euphorbiaceae are characteristic in their epitropous orientation and the presence of an obturator that fits over the micropyle of one or both ovules and fills the gap between the stylar conducting tissue and the nucellus. Within the Phyllanthoideae, some taxa (e.g., *Aporusa, Drypetes*) have a single massive obturator, while others (e.g., *Andrachne, Phyllanthus*) have tenuous separate obturators. Schweiger (1905) surveyed the variation in ovular form in the Euphorbiaceae and found it to be of considerable importance systematically. In some Phyllanthoideae, especially tribe Phyllantheae, the ovules are distinctly hemitropous, instead of anatropous as in the great majority of genera in the family. Singh (1962) has contrasted the anatropous and hemitropous types and illustrated an unusual variation in *Trevia*, where the ovule is ventrally adnate to the placenta and lacks a distinct funicle. The ovules of *Croton* and *Trevia* illustrated by Singh are characteristic of the subfamilies Crotonoideae and Acalyphoideae respectively; in the Crotonoideae the ovule tends to be elongated and has a nucellar beak projecting beyond the micropyle, whereas in the Acalyphoideae the ovule is less elongated with a thickened inner integument and without a projecting nucellus. Ovules in the Euphorbioideae conform to those of the Acalyphoideae.

Considerable embryological work has been done on the Euphorbiaceae (Davis, 1966; Rao, 1970), showing that embryo sac development is of the normal *Polygonum* type in most of the family. Aberrant development has been reported only in the Acalyphoideae and Euphorbioideae: disporic (*Allium*) types occur in *Chrozophora* and *Euphorbia*, and tetrasporic types in *Acalypha, Euphorbia*, and *Mallotus*. A characteristic of most euphorbiaceous female gametogenesis is the early disappearance of the antipodals, which in the older literature led to a number of misinterpretations of embryo sac development in genera such as *Phyllanthus* and *Codiaeum* (Maheshwari, 1942). Apomixis is rare in Euphorbiaceae, even though the earliest report of apogamy is from the genus *Coelebogyne* (Smith, 1841); it has been verified mainly in temperate species of *Euphorbia* such as *E. dulcis* L. (Carano, 1926; Cesca, 1961; Kapil, 1961).

D. FRUIT AND SEEDS

The fruit in most Euphorbiaceae is an explosively dehiscent schizocarp, but indehiscent fruits have evolved repeatedly in all of the subfamilies. The schizocarpous fruit appears to be the primitive state, both in the family as a whole and within individual genera. In *Phyllanthus* (Webster, 1956-1958) there is a particularly complete morphological series: typical capsules (most sections) to baccate fruits (sect. *Anisonema*), drupaceous but dehiscent (sect. *Emblica*), and finally drupaceous and indehiscent (sect. *Cicca*). It must be admitted, however, that this linear sequence does not clearly represent morphological transition within a single phyletic line.

Berg (1975a, b) has provided the most thorough description of the development, anatomy, and ecology of the typical euphorbiaceous fruit as represented in the Australian genus *Micrantheum*. Berg related many of the distinctive features of the euphorbiaceous pistillate flower, such as the vascular pattern in the columella, to adaptive aspects of fruit dehiscence and seed dispersal. He regarded the placentation in *Micrantheum* as not typically axile because the three columellar bundles lie on different radii from the dorsal bundles; he thus described the columellar portion of the axis of the ovary as "an internal carpophore congenitally fused with down-hanging lobes from carpels attached to its tip." However, as shown in the descriptions and illustrations of Venkata Rao & Ramalakshmi (1968), the three basal central strands in the axis each give rise to paired strands that represent the ventrals of the carpel margins; this strongly implies that the placentation in the euphorbiaceous flower is typically axile, and Berg's ingenious hypothesis is unnecessary.

Another provocative suggestion of Berg is that the primary function of the obturator is not to facilitate passage of the pollen tube but rather to displace the seed lower into the coccus for more

effective seed dispersal. Against this view may be cited the great variation in obturator dimensions within the capsular-fruited taxa (although it is possible that size variation could be correlated with differential growth of the ovary overall).

Euphorbiaceous seeds show variation in size, shape, seed-coat ornamentation and anatomy, endosperm development, and configuration of the embryo; seed characters are taxonomically important, especially at specific and generic levels. In the biovulate taxa, there are typically two seeds per locule, but the number is often reduced to one (e.g., in *Amanoa, Meineckia,* and *Savia*). In biovulate taxa with drupaceous fruits, only one or two seeds per fruit may develop (e.g., in *Antidesma, Aporusa, Baccaurea,* and *Drypetes*). Seed size varies greatly, from less than 1 mm in herbaceous species of *Chamaesyce* or *Phyllanthus* to over 4 cm in *Hevea* and *Omphalea.*

Netolitzky (1926), Wunderlich (1968), and Corner (1976) have shown that the anatomical structure of the seed coat is of considerable importance in relating the Euphorbiaceae to other families, as well as providing clues about infrafamilial relationships. The testa (from the outer integument) persists in the mature seed and sometimes is thickened and fleshy (e.g., in *Baccaurea, Mallotus, Margaritaria, Melanolepis, Sapium,* and *Tetrorchidium*). The mechanical layer of the seed is formed from the outer epidermis of the tegmen (inner integument), and Corner reported that it is different in the uniovulate and biovulate taxa. In the Phyllanthoideae, the mechanical cells consist of cuboid (or only slightly radially elongate) sclerotic cells or of tangentially elongated fibers. In contrast, in the uniovulate taxa the mechanical layer is usually formed of radially elongated palisade sclerenchyma ("Malpighian") cells. On the basis of this difference in seed structure, Corner referred the uniovulate taxa (Crotonoideae sensu Pax) to a Malvalean affinity and the Phyllanthoideae to a Celastralean affinity, but frankly admitted that the picture is not crystal-clear.

In my opinion, the primitive condition in the family would seem to be the fibrous exotegmen as found in Phyllanthoideae such as *Andrachne, Antidesma, Aporusa, Baccaurea,* and *Briedelia.* The palisade cells in *Glochidion* seem to be derived from the shortened fibers found in *Breynia, Flueggea,* and *Phyllanthus*; but contrary to Corner's interpretation, the condition in *Glochidion* does not seem to be transitional to that found in the uniovulate taxa. Instead, the tegmen with cuboidal mechanical cells of *Drypetes* may be closer to the main line of specialization. Although the uniovulate subfamilies differ from the Phyllanthoideae in sometimes having tegmic vascular bundles, this character is inconsistent: Corner's groups 1 and 3 contain representatives of all three uniovulate subfamilies, and group 2 contains both Acalyphoideae and Crotonoideae. Nevertheless, it is quite possible that this character is phylogenetically significant. Most of the genera with tegmic vasculature belong to the Crotonoideae, and *Gelonium,* with a "tegmic pachychalaza," may be closest to the ancestral condition.

Although the caruncle is by no means a ubiquitous feature of the euphorbiaceous seed—Baillon (1873) censured Mueller for using it as a generic character—it still is of considerable taxonomic and evolutionary interest. Bresinsky (1963) and Berg (1975a, b) described the structural and functional features of the caruncles in *Euphorbia* and *Micrantheum.* As Schweiger (1905) demonstrated, the caruncle always arises from the micropylar region (exostome) of the outer integument. In *Euphorbia, Micrantheum,* and doubtless the other genera with carunculate seeds, the caruncle functions as an elaiosome to attract ants for dispersal. Berg noted that in *Micrantheum* it may also play a role in the build-up of tension within the developing capsule, leading up to the explosive dehiscence.

Carunculate seeds have been recorded from all of the subfamilies except the Phyllanthoideae (and even in that subfamily there are sometimes micropylar outgrowths that could be regarded as incipient caruncles). However, their distribution within each subfamily is inconsistent; closely related genera may differ in presence or absence of a caruncle, while in various genera (e.g., *Euphorbia, Stillingia*) some species have a caruncle and others lack it. Caruncles are invariably lacking on seeds from indehiscent fruits, which accounts for part (but by no means all) of the spottiness in reports of distribution.

A seed character that appears particularly important in the Phyllanthoideae is the presence or absence of endosperm, which develops as the Nuclear type (Rao, 1970). It is copious in most genera, but scanty or absent in relatively primitive genera such as *Actephila, Amanoa, Spondianthus,* and *Wielandia.* In exalbuminous seeds, the cotyledons are often distinctly folded. Outside the Phyllanthoideae, seeds normally have well-developed endosperm, but there are a few exceptions (e.g., *Elateriospermum* in the Crotonoideae).

Cotyledon characters have been given exceptional weight in the classification of Euphorbiaceae since they were strongly emphasized by Mueller

(1866), who erected his two primary infrafamilial divisions, Platylobeae and Stenolobeae, on the basis of cotyledon shape. Baillon (1873) rightly objected to this overemphasis on the cotyledon character, and his rejection of Mueller's scheme has been substantiated by the palynological studies of Erdtman (1952), Punt (1962), and Köhler (1965), which clearly demonstrated that the Stenolobeae are an artificial group. One can sympathize with Bentham (1880) in his decision to maintain the Stenolobeae as a tribe because of the striking correlation between cotyledon shape, ericoid habit, and Australasian distribution. As a matter of fact, it is still not clear why the character of narrow cotyledon shape should be almost confined to Australia, except for the anomalous North American genus *Reverchonia* (Webster & Miller, 1963).

E. CYTOLOGICAL CHARACTERS

Perry (1943) was the first to provide a survey of chromosome numbers for the Euphorbiaceae, but his sample was very small, and a considerable number of his counts have proved to be erroneous. Three decades later, Hans (1973) presented a much more extensive (and reliable) survey of chromosome numbers; and there have been a few additional surveys since then, such as that of Urbatsch et al. (1975). Although the percentage of species sampled is still very low (below 5%), there are now data on a sufficient number of genera to discuss the possible implications for phylogeny and classification. Hans concluded that there are two fundamental basic numbers in the family: $x = 7$ and $x = 13$, of which the latter is presumed to be derived from the first by doubling and aneuploid reduction. Although this scenario cannot be disproved, it is notable that $x = 13$ is the prevailing number in the "lower" Phyllanthoideae, and it seems unwarranted to invoke a hypothetical ancestral complement of $x = 7$. Hans's reason for doing so is probably a consequence of his following Bentham's (1880) tribal arrangement, and unfortunately the worst mistake in Bentham's treatment is his inclusion of the Buxaceae (with $x = 7$) as one of the tribes.

Hans (1973) is probably correct in concluding that $x = 11$ is the original base number in the Acalyphoideae and Crotonoideae. The same conclusion can also be made for the Euphorbioideae, as $x = 11$ is prevalent in the Hippomaneae. Hans regarded $x = 7$ and 10 as the primary base numbers for *Euphorbia*, but this implies that the genus is polyphyletic, which is scarcely warranted. In my opinion, the evidence clearly suggests an original number of $x = 10$, with other numbers originating in a descending aneuploid series. Jones & Smith (1969) reported a surprising diversity of basic numbers in *Monadenium*: $x = 12$, 16, 17, 18, and 19. Since the prevalent number in *Monadenium* is $x = 18$, and the lowest number of $x = 12$ occurs in a species (*M. echinulatum* Stapf) ranked as highly specialized in the monograph of Bally (1961), the most probable hypothesis is that these numbers are of polyploid origin from an ancestor with $x = 9$, followed by a mostly decreasing aneuploid series. Unfortunately, all of the cytologically known potential succulent ancestral species in *Euphorbia* subg. *Euphorbia* are reported to have $x = 10$, so the case remains not proven.

SUMMARY OF TAXONOMIC CHARACTERS IN THE EUPHORBIACEAE

At this writing, only one comprehensive phylogenetic analysis of Euphorbiaceae using both phenetic and cladistic methods has been made. Levin (1986b, c) classified the genera of subfamily Phyllanthoideae primarily on the basis of leaf anatomical data. A cladistic study of Oldfieldioideae based on pollen characters has recently been completed (Levin & Simpson, 1994a, b). However, critical phylogenetic analysis of the family is really just beginning. Considerably more morphological, anatomical, and biochemical (not to mention molecular) work needs to be done before the data set is adequate.

In Table 1 are listed a basic set of primitive and derived character states for the Euphorbiaceae, based on both the literature and personal observations. It is focused on the Phyllanthoideae as the sister group of the other subfamilies, and also the sister group of the unknown collateral (or ancestral) closest related family. I have used a pastiche of several potential "ancestral" families as a composite sister group; this includes families of Linales and Sapindales (sensu Cronquist, 1981) such as Ixonanthaceae, Irvingiaceae, and Linaceae. The ovular structure in these Linales is suggestively similar to that in the Euphorbiaceae (Webster, 1967). Other possible families, such as the Thymelaeaceae, should be tested as sister groups, and this might well alter the list of characters.

Further refinement of this crude and preliminary list of character states in Euphorbiaceae can be expected from more intensive study of fossils as well as living plants. Since I reviewed the earlier reports of euphorbiaceous fossils (Webster, 1967), data provided by fossil wood and fruits has been supplemented by discoveries of euphorbiaceous

flowers in the Eocene. Crepet & Daglian (1982) have described a genus *Hippomaneoidea* from the Eocene Claiborne formation that appears similar to the modern genus *Senefeldera*. This raises the encouraging possibility that further discoveries may provide a picture of the past evolution of euphorbiaceous reproductive structures and a firmer basis for polarizing character states. Although the systematic affinities of fossil fruits have proved more difficult to establish, the study of Mazer & Tiffney (1982) on fruits of Hippomaneae from the North American Eocene indicates that it may be possible to correlate flower and fruit characters in fossil taxa of Euphorbiaceae.

The Ecological and Biogeographic Background

1. pollination

Despite the reproductive diversity in the Euphorbiaceae, the limited studies on pollination indicate that the flowers of the majority of genera are not highly specialized for a single kind of pollination vector. Although wind pollination is presumably the norm in a limited number of genera (e.g., *Acalypha, Macaranga, Mallotus*) with anemophilous characteristics such as reduced perianth and nectar, it has been demonstrated experimentally only in a few genera such as *Mercurialis* (Daumann, 1972) and *Ricinus* (Alex, 1957). Perhaps the typical situation might be that demonstrated for three species of *Chamaesyce* in Arizona by Ehrenfeld (1976), who collected 175 species of insects, including small bees, flies, and wasps. A similar spectrum of visitors was reported for a North American and a South American species of *Jatropha* by Simpson (1977), and for *Jatropha gossypiifolia* L. in India by Reddi & Reddi (1983). Steiner (1983) reported visits by a variety of bees, flies, and butterflies to the flowers of *Croton draco* Cham. & Schltdl. in Panama. Recently it has been claimed (Dominguez & Bullock, 1989; Dominguez et al., 1989) that the Mexican species *Croton pseudoniveus* Lundell and *C. suberosus* HBK are wind-pollinated, even though nectaries are present in both staminate and pistillate flowers. The argument is made that the role of nectar in *Croton suberosus* is to attract wasps that deter lepidopteran predators from attacking the foliage. However, other reports such as that of Jose & Inamdar (1989) on the role of floral nectaries in *Croton bonplandianus* Baill. support adaptation for insect pollination. In my opinion, the arguments for wind pollination in *Croton*, in view of the floral and pollen morphology, are not entirely persuasive; Dominguez and his collaborators have not yet demonstrated convincingly that the benefit from visits of *Polistes* wasps is not merely incidental (or superfluous) with respect to a pollination system that depends on visitations by a variety of generalist visitors. It should be noted, though, that *Eremocarpus*, a specialized derivative group surely derived from within *Croton* (and better treated as a section of that genus), does appear to be wind-pollinated. The situation in *Croton suberosus* could represent a preliminary step toward anemophily and merits further experimental study.

The lack of specificity in most euphorbiaceous flower/pollinator relationships clearly has not impeded diversification in floral and inflorescence structure; however, the number of genera that have received even superficial study is very small. A number of instances of more unusual adaptations for pollination have been demonstrated, and no doubt many remain to be detected. Pollination by Diptera is no doubt usually unspecialized, as recorded by Hauman-Merck (1912) for a species of *Sapium* in Argentina, where species of genera such as *Eristalis* and *Sarcophaga* were recorded removing nectar from extra-floral nectaries on the floral bracts; as Hauman suggested, a similar syndrome may occur in other taxa of tribe Hippomaneae, but there are few recent observations. In contrast to this, however, Warmke (1952) demonstrated that *Hevea* in Brazil is naturally pollinated by midges (Heleidae). Although further verification of this is desirable, it appears that *Hevea* may depend on midges of a single family for pollination, and this might well prove to be the case for other euphorbiaceous genera.

In a few genera of Euphorbiaceae, floral structure has become modified for pollination by Lepidoptera. Perkins et al. (1975) reported nocturnal pollination of *Cnidoscolus texanus* (Muell. Arg.) Small in Oklahoma by two species of hawkmoths. However, Breckon, in observations on four species of *Cnidoscolus* in Mexico (pers. comm.), found pollination primarily by sphingids in *C. herbaceus* (L.) I. M. Johnston, but mostly by butterflies in *C. aconitifolius* (Miller) I. M. Johnston and *C. multilobus* (Pax) I. M. Johnston; the most important butterfly families were Papilionidae and Nymphalidae, but significant numbers of visits were made by taxa of Heliconidae, Pieridae, and Hesperiidae. In Brazil the situation in *Cnidoscolus* is similar, except that near Jequié, Bahia, visits to *Cnidoscolus urnigerus* Pax were seen to be almost entirely by hummingbirds (Webster, unpublished). The peculiar urn-shaped corolla and the androecium of

distinct (not monadelphous) stamens appear to have evolved in this one species concomitantly with a shift from lepidopteran to ornithophilous pollination.

Pollination by small Hymenoptera is doubtless very widespread in the Euphorbiaceae. In California, wasps were found to be the most important pollinators for *Croton* and *Euphorbia* by Moldenke (1976). In Suriname, pollination of *Tragia lesser-tiana* (Baill.) Muell. Arg. appeared to be primarily by *Melipona* (Webster & Dobson, unpublished), although species of *Trigona* were common visitors to this and other Euphorbiaceae. Further observations of pollination by small wasps and bees may help to elucidate some of the variations in euphorbiaceous floral structure that at present appear mysterious.

Larger bees presumably are major pollinators for Euphorbiaceae with relatively large and showy flowers, such as *Aleurites*, *Manihot*, and species of *Croton*; however, critical field observations are still almost entirely lacking. The major exception involves *Dalechampia*, which has small flowers aggregated into a conspicuous pseudanthium that in most species produces resin for a floral reward (Webster & Webster, 1972). Armbruster & Webster (1979) demonstrated that in Mexico pollination of one species, *Dalechampia magnistipulata* Webster & Armbruster, was affected by female euglossine bees visiting the inflorescence to gather the resin; in the other species, *D. spathulata* (Scheidw.) Baill., which has modified resin glands, visits were by male euglossine bees gathering volatile terpenoids. Subsequently, in a series of papers Armbruster (1984; 1988; Armbruster & Herzig, 1984) described pollination of a large number of *Dalechampia* species, which depend on visits by anthidiine and euglossine bees. The considerable speciation in *Dalechampia* (over 100 species) may plausibly be related to exploitation of this unique "niche" in the pollination spectrum of tropical plants. Armbruster (1992) showed a fascinating correlation between phylogeny of taxa in *Dalechampia* and evolution of pollination mechanisms; he convincingly demonstrated that pollination by fragrance-collecting euglossine bees has evolved independently in three different species lineages.

The other major occurrence of pseudanthial inflorescences in the Euphorbiaceae is in the tribe Euphorbieae, where modification of floral structure has occurred along an entirely different pathway. As indicated by Venkata Rao (1971), the inflorescence structure of *Dalechampia* may be derived from the thyrse of Acalypheae, in which the floral bracts are usually glandless. In contrast, the cyathium of the Euphorbieae appears derived from the spicate thyrse of the Hippomaneae, in which the nectaries of the floral bracts have become incorporated as the nectaries of the pseudanthium; theories about the nature of the cyathium have been reviewed by Dressler (1957) and Webster (1967). Other pseudanthia, of quite a different nature, are known in *Uapaca* (Phyllanthoideae) and *Pera* (Acalyphoideae); but nothing is known about their reproductive biology.

The pseudanthium of *Euphorbia* and *Chamaesyce* is generally pollinated by small generalist insects (flies, wasps, bees) as reported by Ehrenfeld (1976) and earlier workers. However, the type species of *Euphorbia* subgenus *Poinsettia*, *Euphorbia pulcherrima*, has very conspicuous red bracts subtending the cyathia (forming a second-order pseudanthium); this, and the copious nectar, suggest hummingbird pollination. Indeed, Dressler (1957) clearly illustrated how the more or less radially symmetrical cyathium of *Euphorbia* has been highly modified into the bilaterally symmetrical cyathium of *Pedilanthus* that is pollinated mainly by hummingbirds.

At least fragmentary accounts of most major pollination syndromes of Euphorbiaceae were published by the end of the 19th century. However, Steiner (1981, 1983) demonstrated mammal pollination of *Mabea occidentalis* Benth. by bats (*Glossophaga*, *Carollia*) and the red woolly possum (*Caluromys*), which visit the inflorescences to obtain nectar from the extrafloral nectaries on the bracts. An even more remarkable instance of bat pollination has been reported by Steiner (1982) in another genus of Hippomaneae, the sandbox tree (*Hura*). In contrast to *Mabea*, in which the staminate and pistillate flowers are associated in the same inflorescence, in *Hura* the fleshy staminate inflorescences and the solitary pistillate flowers with bizarrely enlarged stigmas behave as separate pollination units. Steiner suggested that the staminate "cones" are taken by bats mistaking them for fleshy fruits—certainly the most striking case of "mistake pollination" in the Euphorbiaceae.

These examples indicate that the great diversity of euphorbiaceous floral structure is at least partly related to a long history of shifting adaptation to different pollinators. However, because the flowers of most Euphorbiaceae are less than 1 cm in diameter, the effective unit of pollination has often been the inflorescence or subinflorescence. Functional studies of evolution of reproductive structures must therefore take into account the inflo-

TABLE 2. Taxonomic distribution of disseminule types in the Euphorbiaceae. A number of genera have not been scored due to lack of definite information.

Subfamily	Number of genera	Seeds carunculate	Seeds ecarunculate	Testa fleshy	Fruit indehiscent
Phyllanthoideae	58	0	38	5	12
Oldfieldioideae	28	11	14	0	2
Acalyphoideae	118	18	77	13	5
Crotonoideae	61	19	29	5	8
Euphorbioideae	42	16	18	1	4
Totals	307	64	176	24	31

rescence as a whole, as well as its constituent parts. Furthermore, as discussed below, adaptations for dispersal may also have a "retrospective" effect in projecting developmental restraints back onto the flowers.

2. DISPERSAL

The prevalent fruit type in the primitive Euphorbiaceae (Phyllanthoideae), and indeed in most of the taxa of the family, is the 3-carpellate schizocarp that dehisces explosively into three segments (cocci) each with one or two seeds. Typically, the central axis of the flower (carpel margins and placentae) remains in the fruit as a columella after the cocci have dispersed. In the subfamily Phyllanthoideae, the individual seeds may have a dry or fleshy testa, but there is never the large conspicuous elaiosome (caruncle) found in other subfamilies; the caruncle appears to be a novelty (independently evolved?) in the subfamilies Oldfieldioideae and Acalyphoideae.

Under the description of fruit and seed morphology, Berg's (1975b) detailed study on the Australian oldfieldioid genus, *Micrantheum*, is mentioned, in which dispersal of the carunculate seeds depended on attraction of ants to the elaiosome. Berg's study remains unique in its synthesis of field observations on ant dispersal of *Micrantheum* seeds with a careful anatomical study of fruit and seed development; he also provided comparative data on myrmecochory in several other Australian genera of Euphorbiaceae (1975a, 1981). Since a very rudimentary elaiosome occurs in some Phyllanthoideae (e.g., *Phyllanthus*), it is not unreasonable to suggest that selection for ant dispersal was an important factor in the evolution of fruit and seed morphology in the Euphorbiaceae. Berg plausibly suggested that the diagnostic character syndrome of the euphorbiaceous gynoecium and fruit—including the reduced ovule number, obturator, the axis becoming a persistent columella, and the closed ventral wall of the coccus—represent a specialized derivation from an ancestral state of nonexplosive capsular fruits, and that morphological changes involved in dispersal have as a consequence relayed from the fruit back into the flower. Berg also suggested, somewhat less persuasively, that this characteristic euphorbiaceous gynoecium/fruit/seed character syndrome arose in a tropical monsoon climate; this could be so, but there are many taxa with typical explosive fruits in the tropical rainforest. Intensive investigations on other genera are badly needed in order to test Berg's hypotheses.

Some of the relationships involved in the adaptive aspects of dispersal are given in Tables 2–4. It is notable from Table 2 that "unspecialized" seeds (i.e., ecarunculate, with dry seed coat) predominate in all five subfamilies. However, in the Oldfieldioideae and Euphorbioideae there are nearly as many carunculate as ecarunculate genera. The Acalyphoideae have the lowest percentage of the four subfamilies with carunculate seeds, but in compensation have the largest number of seeds with fleshy testa.

Geographically (Table 3), there are some interesting differences in average dispersal type, since the neotropical and Australasian genera have many more myrmecochorous genera than ornithochorous, whereas in the rest of the paleotropical area the situation is reversed.

In view of the interest tropical ecologists have taken in the role of dioecy as a reproductive adaptation, it is of some interest to compare the types of fruits and seeds with the monoecious versus dioecious conditions within Euphorbiaceae (Table 4). The data support the predictions of Bawa (1980), Givnish (1982), and Steiner (1988) that dioecious taxa should have a higher percentage of ornitho-

TABLE 3. Relation of dispersal type to geographic distribution of genera: carunculate seeds are treated as myrmecochorous; fleshy seeds and indehiscent fruits as ornithochorous. Many genera, not enumerated in the table, are probably autochorous.

	Myrmecochorous	Ornithochorous
Neotropics	18	10
Africa/Madagascar	8	21
Tropical Asia	6	28
Australasia	21	6
Holarctic	4	0
Totals	57	65

chorous disseminules than do monoecious taxa. In contrast, there appears to be no significant difference in the expectation of monoecy or dioecy in myrmecochorous taxa, or in the "unspecialized" taxa, which are presumably mostly autochorous.

Although Berg is surely correct in suggesting that the autochorous tricoccous fruits represent a primitive state, and myrmecochory developed subsequently, further evolution to fleshy, more or less indehiscent fruits has occurred in all of the subfamilies. Within the Phyllanthoideae there are also a number of fruits that appear adapted for dispersal by birds: examples include berries in *Breynia*, and drupes in *Drypetes* and *Uapaca*. In *Phyllanthus* (Webster, 1956), there is a particularly marked progression from schizocarps (subgenus *Isocladus*) to berries (subgenus *Kirganelia*) and finally to drupes (subgenus *Cicca*). Within dry fruits, there has also been an elaboration of seeds with sarcotesta; this is very often reddish, as in *Macaranga* or Mallotus, but in *Margaritaria* it is blue or green. The baccate fruits in Euphorbiaceae are watery and dispersed by nonspecialist frugivores (Snow, 1981). Presumably, drupaceous fruits are dispersed by specialist frugivores, but we have very little data on Euphorbiaceae. A striking development in Acalyphoideae and Crotonoideae is the evolution of large oily seeds in genera such as *Caryodendron*, *Hevea*, *Joannesia*, *Aleurites*, and *Omphalea*. The seeds of *Hevea* are explosively dispersed to great distances (up to 45 m according to van der Pijl, 1982) and then dispersed by rivers in the Amazon basin. *Hevea* and these other large-seeded taxa are mostly rainforest dominants (*Omphalea* is a liana), but another group of genera such as *Homonoia*, rheophytes that are adapted to extensive periods of submergence, also presumably depend mainly on water dispersal. According to Gottsberger (1978), none of the Euphorbiaceae observed in the Amazon basin (including *Hevea*) are dispersed by fish, but rather the seeds are preyed upon. Wind dispersal is rare in Euphorbiaceae and occurs mainly in taxa with samaroid fruits adapted for open tropical woodland (e.g., *Hymenocardia*); there are no good examples of winged seeds in the Euphorbiaceae.

Bresinsky (1963), on the basis of studies of elaiosomes, hypothesized that seed morphology in temperate taxa with myrmecochory has been derived from ornithochory in tropical taxa. This assumes that seeds with sarcotesta (tropical forms) have evolved into carunculate seeds (temperate forms), with *Mercurialis* showing an intermediate condition. However, the real situation appears much more complex. Primitively, seeds in the Euphorbiaceae appear to have been ecarunculate, and well-developed caruncles are unknown in the Phyllanthoideae. It is interesting that carunculate seeds occur in "basal" taxa of the Oldfieldioideae (*Tetracoccus*), Acalyphoideae (*Clutia*), and Crotonoideae (*Micrandra*, *Manihot*). Seeds with sarcotesta are found in relatively "advanced" genera (e.g., *Margaritaria*, *Breynia*) in Phyllanthoideae, but in relatively "basal" genera in Acalyphoideae (*Cheilosa*) and Crotonoideae (*Tetrorchidium*, *Klaineanthus*). It appears that diaspore evolution has followed a tortuous path, with many reversals between dry/fleshy and carunculate/ecarunculate testa. There is a general tendency for seeds with sarcotesta to occur in closed forested habitats and for those with caruncules to occur in open dry habitats. What is evident, however, is there is no unilinear direction

TABLE 4. Relation of sexual expression to dispersal type in genera of Euphorbiaceae. M indicates genus is monoecious; M/D, monoecious or dioecious (in same or different species of a genus); D, consistently dioecious.

Subfamily	Seeds dry (autochorous)	Seeds carunculate (myrmecochorous)	Seeds/fruits fleshy (ornithochorous)	Totals for each subfamily
Phyllanthoideae				
M	11	0	3	14
M/D	5	0	1	6
D	22	0	9	31
Oldfieldioideae				
M	1	3	0	4
M/D	1	1	0	2
D	12	7	3	22
Acalyphoideae				
M	44	4	6	54
M/D	3	0	1	4
D	30	14	11	55
Crotonoideae				
M	15	13	4	32
M/D	0	2	0	2
D	14	4	9	27
Euphorbioideae				
M	14	13	0	27
M/D	2	2	1	5
D	2	1	4	7
Totals				
M	85	33	13	131
M/D	11	5	3	19
D	80	26	36	142
	176	64	52	292

TABLE 5. Summary of diversity in subfamilies and tribes of Euphorbiaceae as measured by numbers of native and endemic genera (endemic genera indicated in parentheses). Tropical Arabia is counted as part of Africa, Pacific islands with Australasia.

Subfamily	America	Africa	Madagascar	Asia	Australasia
Phyllanthoideae					
Wielandieae	4 (3)	4 (3)	3 (2)	1 (0)	1 (0)
Amanoeae	1 (0)	2 (1)			
Bridelieae		2 (0)	2 (0)	2 (0)	2 (0)
Phyllantheae	8 (3)	14 (4)	6 (1)	10 (1)	7 (0)
Drypeteae	1 (0)	3 (2)	1 (0)	2 (1)	1 (0)
Antidesmeae	6 (5)	7 (4)	4 (1)	4 (1)	5 (2)
Hymenocardieae	1 (1)	1 (0)		1 (0)	
Bischofieae				1 (0)	1 (0)
Totals	21 (12)	33 (14)	16 (4)	21 (3)	17 (2)
Oldfieldioideae					
Croizateae	1 (1)				
Podocalyceae	3 (3)				
Caletieae		1 (1)		2 (1)	13 (12)
Picrodendreae	4 (4)	4 (3)	3 (2)	1 (1)	
Totals	8 (8)	5 (4)	3 (2)	3 (2)	13 (12)
Acalyphoideae					
Clutieae		1 (1)			
Pogonophoreae	1 (0)	1 (0)			
Chaetocarpeae	1 (0)	1 (0)	1 (0)	2 (1)	
Pereae	1 (1)				
Cheiloseae				2 (1)	1 (0)
Erismantheae				3 (2)	1 (0)
Dicoelieae				1 (1)	
Galearieae		2 (1)		2 (0)	1 (0)
Ampereae					2 (2)
Agrostistachydeae		2 (2)		2 (1)	1 (0)
Chrozophoreae	5 (4)	2 (0)		6 (4)	1 (0)
Caryodendreae	2 (2)	1 (1)			
Bernardieae	2 (2)	2 (2)		1 (1)	
Pycnocomeae		2 (1)	2 (1)	4 (2)	2 (0)
Epiprineae		2 (1)	2 (0)	8 (6)	
Adelieae	4 (4)	1 (1)			
Alchorneae	5 (4)	1 (0)	3 (2)	1 (0)	2 (2)
Acalypheae	3 (1)	11 (6)	10 (5)	14 (4)	11 (3)
Plukenetieae	11 (8)	3 (1)	3 (1)	5 (3)	
Omphaleae	1 (0)	1 (0)	1 (0)	1 (0)	1 (0)
Totals	36 (26)	33 (17)	22 (9)	52 (26)	23 (7)
Crotonoideae					
Micrandreae	4 (4)				
Manihoteae	2 (2)				
Adenoclineae	3 (2)	3 (2)		1 (0)	
Gelonieae		1 (0)	1 (0)	1 (0)	1 (0)
Elateriospermeae				1 (1)	
Jatropheae	3 (2)	2 (1)		3 (2)	
Codiaeae	4 (4)	1 (0)		8 (5)	5 (3)
Trigonostemoneae				1 (0)	1 (0)
Ricinocarpeae				1 (1)	6 (6)
Crotoneae	4 (3)	2 (1)	1 (0)	2 (1)	1 (0)
Ricinodendreae		2 (1)	1 (0)	1 (0)	
Aleuritideae	2 (2)	7 (6)	3 (2)	4 (3)	1 (0)
Totals	22 (19)	18 (11)	6 (2)	23 (13)	15 (9)

TABLE 5. Continued.

Subfamily	America	Africa	Madagascar	Asia	Australasia
Euphorbioideae					
Stomatocalyceae	1 (1)	2 (2)		1 (0)	1 (0)
Hippomaneae	14 (10)	4 (2)	1 (0)	5 (1)	4 (0)
Pachystromateae	1 (1)				
Hureae	4 (4)				
Euphorbieae	4 (2)	7 (4)	3 (0)	2 (0)	4 (2)
Totals	24 (18)	13 (8)	4 (0)	8 (1)	9 (2)
Grand totals	111 (83)	102 (54)	51 (17)	107 (45)	77 (32)

of seed-coat specialization in any of the subfamilies except for the Phyllanthoideae, which lack myrmecochory, and the Oldfieldioideae, which are overwhelmingly myrmecochorous (Table 2). The geographical distribution of myrmecochorous and ornithochorous diaspores (Table 3) is interesting, with the neotropical and Australian regions mainly myrmecochorous, and the paleotropical region ornithochorous. Particularly notable is the prevalence of seeds with fleshy testa in the paleotropical region, and the overwhelming predominance of myrmecochorous dispersal in Australia, confirming the statements of Berg (1975a, b, 1981).

Little has been studied so far on the effects of seed predation on dispersal systems in Euphorbiaceae. The seed-coat toxins of such genera as *Ricinus* could be explained as a deterrent to predators, but this apparently has not been studied in the field in Africa, where natural predators might be expected. However, there is a suggestive study by Cook et al. (1971) on the effects of seed predation by doves on the seed morphology of *Croton setigerus* Hook. in California. Here there is a kind of "balanced polymorphism" between gray unpatterned seeds with toxins produced by plants in the deserts and mottled palatable seeds that are produced by coastal populations. Cook et al. (1971) argued plausibly that the mottled seed patterns of coastal plants are maintained by the adaptive advantage of camouflage, whereas the unpatterned seeds of desert areas indicate lower levels of predation. The situation is reminiscent of that in *Ricinus*, which also has notoriously variable seed-coat patterns.

3. GEOGRAPHIC DISTRIBUTION

A detailed analysis of the geographic distribution patterns of the 50 tribes of Euphorbiaceae is clearly beyond the scope of this essay. However, it seems appropriate here to outline some of the major geographic patterns of the five subfamilies and indicate some of the most striking disjunct or relict distributions. There do not appear to be any critically documented maps of suprageneric taxa in the literature, and since the discussion of Bentham there have been few analyses besides the study of the distribution of Jatropheae by Pax (1910), and (partially) of the Euphorbieae by Croizat (1972) and Leach (1976).

A review of the geographic distribution of the tribes and genera of subfamily Phyllanthoideae brings out the striking prominence of Africa and Madagascar (Table 5). The highly disjunct distribution of the primitive genus *Savia* is striking (Fig. 1); including the related genus *Heywoodia*, the diversity in Africa/Madagascar is clearly greater than the New World. The occurrence of the relict genus *Wielandia* in Madagascar and the Seychelles is noteworthy; together with the endemic genera *Blotia* and *Petalodiscus*, it indicates a major center in Malagasia (Fig. 2). *Discocarpus* and *Lachnostylis* apparently form a vicariant pair in South America and Africa, and the neotropical and paleotropical species of *Savia* seem equally vicariant. This South American/African disjunction is repeated at the level of groups of species within a number of other genera of Phyllanthoideae, such as *Amanoa*, *Drypetes*, *Margaritaria*, *Meineckia*, and *Phyllanthus*. It also occurs in other subfamilies, as noted in Table 5. It seems particularly informative to look at the distribution of the more primitive genera within each subfamily. It is notable that in the Oldfieldioideae the "basal" tribes Croizateae and Podocalyceae are entirely neotropical (Fig. 3), whereas the Caletieae are entirely Old World, and only the Picrodendreae (Fig. 4) are represented in both hemispheres. Within the Picrodendreae, the genera *Celaenodendron*, *Piranhea*, and *Oldfieldia* appear to be vicariants that link America and Africa in the manner of *Savia*. The Laurasian genus *Tetracoccus* is taxonomically isolated, but clearly seems to belong in the Podocalyceae; it may represent the taxon in which the important

FIGURE 1.[3] Distribution of Phyllanthoideae, tribe Wielandieae: 1, *Heywoodia* (dotted line, Africa); 2, *Savia* (continuous line); 6, *Actephila* (dashed line); 9, *Chonocentrum* (dotted line, America).

apomorphy of carunculate seeds first appeared in the family.

In the Acalyphoideae, there is one relict neotropical/African genus, *Pogonophora*, one of east and southern Africa, *Clutia*, one neotropical and Asiatic, *Chaetocarpus*, and three Asiatic, *Cheilosa*, *Neoscortechinia*, and *Trigonopleura* (Figs. 5, 6). Africa does not appear to be the epicenter for oldfieldioids and especially acalyphoids that it is for the Phyllanthoideae. It is notable that in the Acalyphoideae, in contrast to the biovulate subfamilies, basal taxa such as Cheiloseae and Chaetocarpeae are well developed in the Oriental region.

The Crotonoideae (Figs. 7, 8) differ from all the other subfamilies in a clear predominance of neotropical relict genera: *Ditta*, *Glycydendron*, *Hevea*, *Micrandra*, *Micrandropsis*, and *Tetrorchidium*. However, *Tetrorchidium* also occurs in Africa, and *Adenocline* and *Klaineanthus* are confined there. The Crotonoideae therefore show considerable parallelism to the Phyllanthoideae, except that the center of gravity is definitely to the west of the Atlantic rather than to the east. Finally, the primitive Euphorbioideae of tribe Stomatocalyceae (Fig. 9) give an ambiguous picture, with one neotropical genus, *Nealchornea*, two African, *Hamilcoa* and *Plagiostyles*, and one oriental, *Pimelodendron*. It is interesting that the "advanced" tribe Euphorbieae (Fig. 10) has a distributional pattern somewhat paralleling the Stomatocalyceae, with tribe Anthosteminae in Africa/Madagascar, the Neoguillauminiinae in Australia/New Caledonia, and the Euphorbiinae (via shrubby species of subg. *Esula*) with an apparent focus in Africa/Madagascar. To me, this suggests that as stated by Raven & Axelrod (1974), deployment of a significant number of tribes of Euphorbiaceae may have taken place before Cretaceous plate tectonic movements separated the taxa of the family into their present disjunct situations. Fossil evidence (summarized for North America by Taylor, 1990) is still limited, but the fact that fossils of the relatively "advanced" tribe Hippomaneae have been recorded from the Eocene (Crepet & Daglian, 1982; Dilcher & Manchester, 1988) suggests that the origin and initial spread of all five subfamilies may go back into the Cretaceous, or the earliest Tertiary. For example, the pollen records from Australasia discussed by Martin (1974, 1978) indicate that relatively "advanced" genera of Oldfieldioideae were in place in Australia in the Paleocene, which surely implies differentiation of the subfamily well back into the Cretaceous.

It is not easy to summarize the overall distributional history of the Euphorbiaceae, but I am struck by the remarkable insightfulness of the essay

[3] Distributions are based on references cited in Webster (1994) and examination of herbarium specimens, primarily at DAV. Genus numbers are the same as in Webster (1994). Distributions are necessarily somewhat generalized and do not show minor gaps.

FIGURE 2.[3] Distribution of Phyllanthoideae, tribe Wielandieae (continued): 3, *Gonatogyne*, (dotted line, Brazil); 4, 5, *Blotia*, *Petalodiscus* (dotted line, Madagascar); 7, *Discocarpus* (dashed line, America); 8, *Lachnostylis* (dashed line, Africa); 10, *Wielandia* (solid line).

by Bentham (1878), who presented the first model for the geographic patterns involved in the origin and radiation of the Euphorbiaceae. Bentham's words deserve to be quoted: ". . . we may be led to conjecture that the most ancient home of the Order was in the Old World, but that several of the principal forms were differentiated and widely spread before that remote period when the present impassible barriers opposed by the Atlantic and Pacific did not exist, or were crossed over in some

FIGURE 3.[3] Distribution of Oldfieldioideae. Tribe Croizateae: 61, *Croizatia*. Tribe Podocalyceae: 62, *Podocalyx*; 63, *Tetracoccus*; 64, *Paradrypetes*.

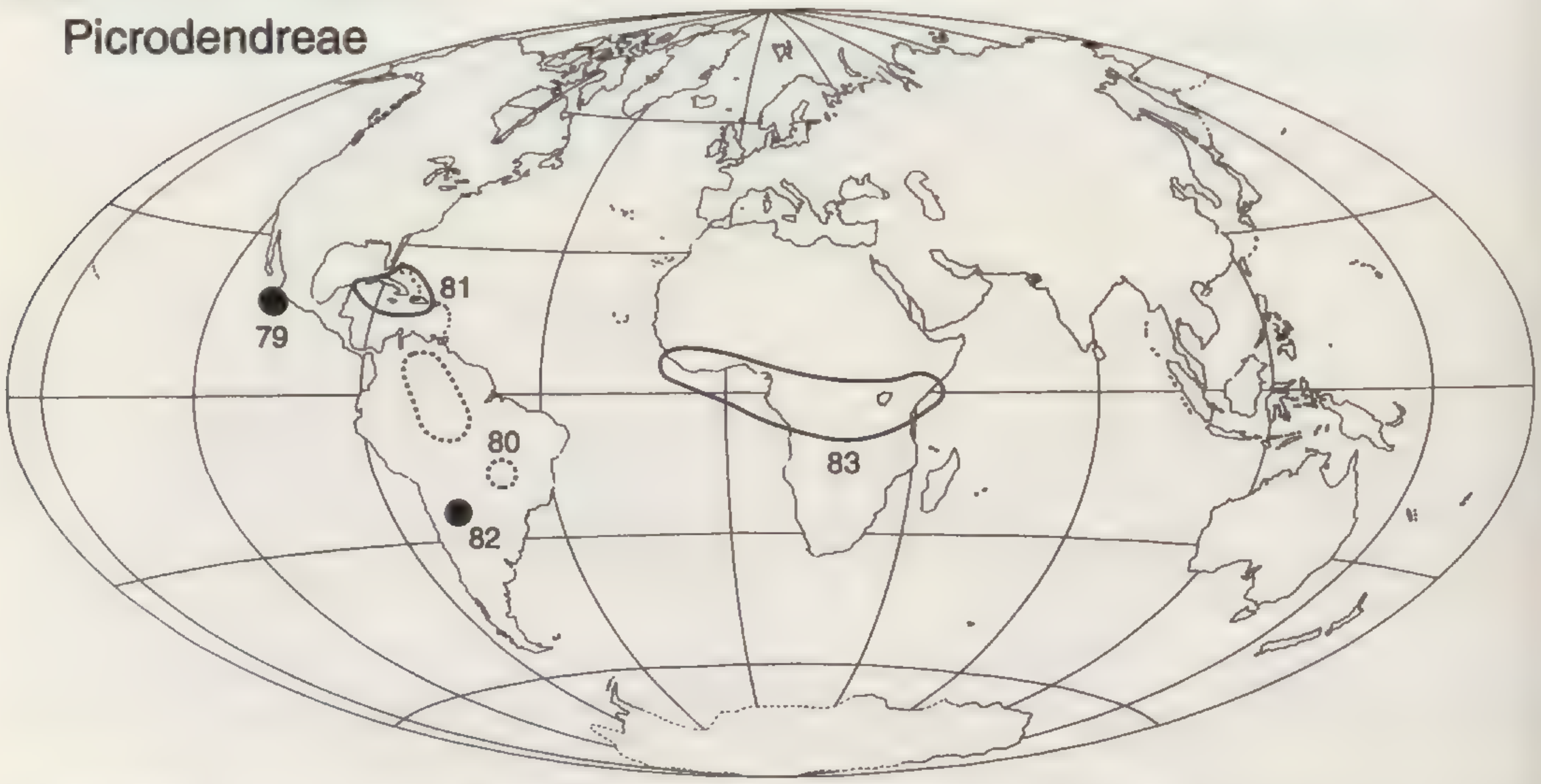

FIGURE 4.[3] Distributions of Oldfieldioideae, tribe Picrodendreae: 79, *Celaenodendron* (dot, North America); 80, *Piranhea* (dashed line); 81, *Picrodendron* (solid line, North America); 82, *Parodiodendron* (dot, South America); 83, *Oldfieldia* (solid line, Africa).

manner of which no plausible explanation has been suggested. It would also appear that interchange of forms between the principal Old-World centres of differentiation . . . continued long after the interposition of the obstacles preventing the spread of the new American forms." Later in this essay Bentham clearly stated "that the most ancient home of the order was in the Old World, whence it spread in very remote times to America."

This scenario proposed by Bentham over a cen-

FIGURE 5.[3] Distribution of Acalyphoideae. Tribe Clutieae: 89, *Clutia* (solid line, Africa). Tribe Pogonophoreae: 90, *Pogonophora* (dashed line). Tribe Cheiloseae (solid line, Asia; ranges of the two genera combined); 94, *Cheilosa*; 95, *Neoscortechinia*.

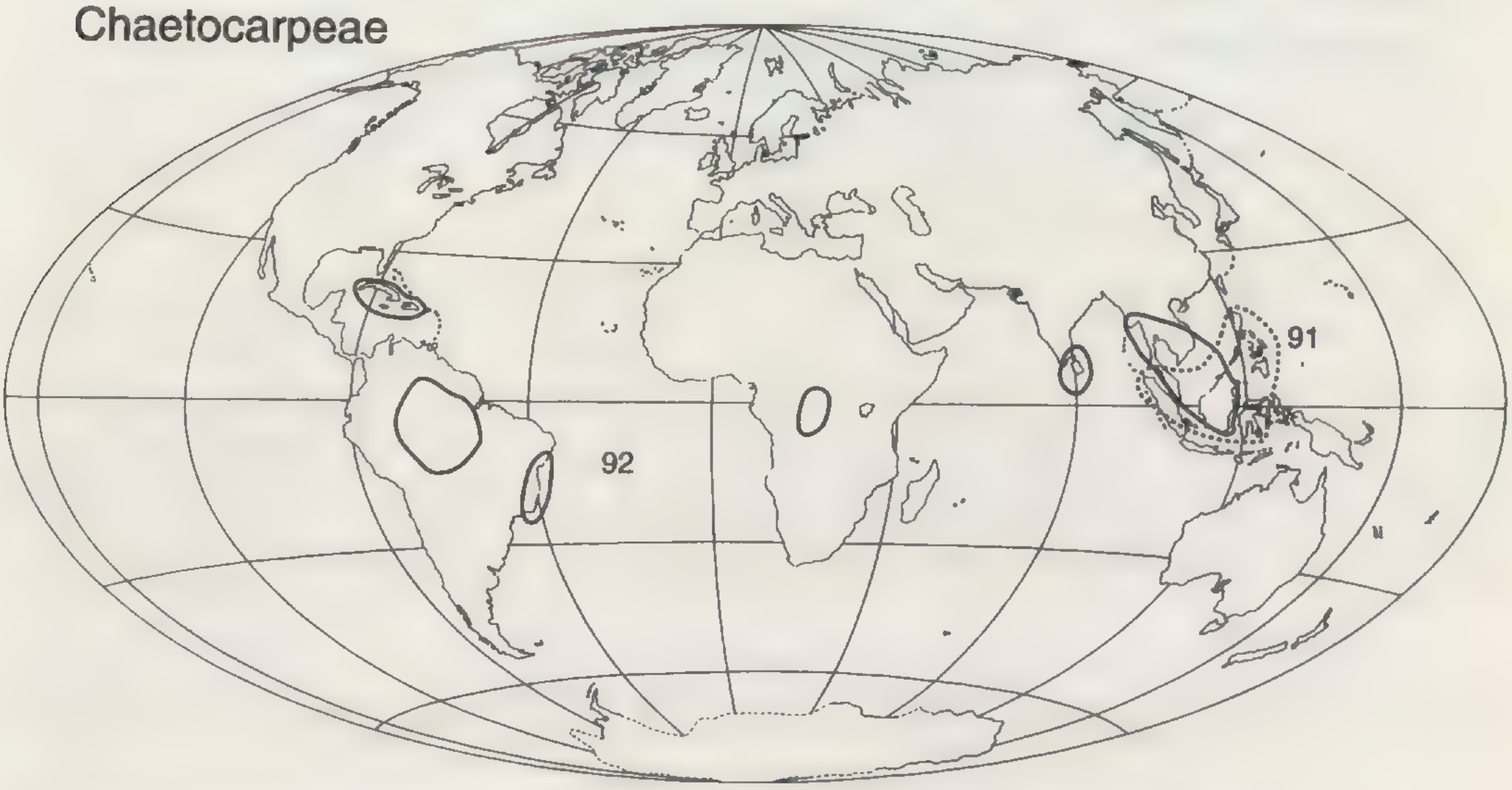

FIGURE 6.[3] Distribution of Acalyphoideae, tribe Chaetocarpeae: 91, *Trigonopleura* (dashed line); 92 *Chaetocarpus* (solid line).

tury ago now appears as a prescient anticipation of models of intercontinental relationships based on plate tectonic models. Pax (1924), although not mentioning Bentham's essay, accepted much the same overall explanation of intercontinental "land bridge" distributions in Euphorbiaceae, and—unlike most plant geographers of his time—did not reject "continental drift" as an explanation. The very limited paleontological record still does not provide critical evidence for Euphorbiaceae, but the distributions and relationships of the taxa are now better understood, so that Bentham's model

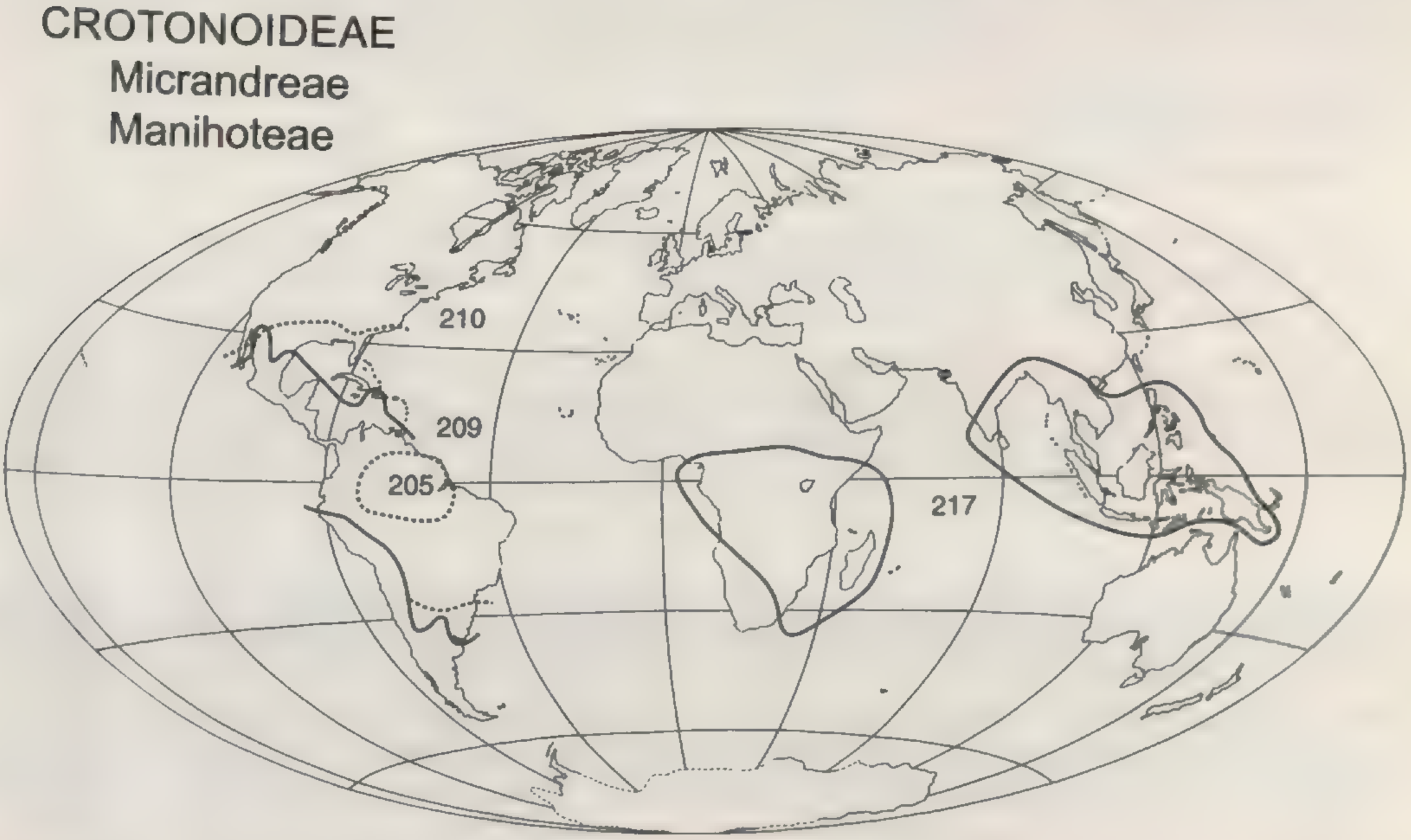

FIGURE 7.[3] Distribution of Crotonoideae. Tribe Micrandreae (dotted line, generic ranges combined); 205, *Micrandra* [and 206, *Micrandropsis*; 207, *Cunuria*; 208, *Hevea*]. Tribe Manihoteae (northern and southern limits): 209, *Manihot*; 210, *Cnidoscolus*. Tribe Gelonieae: 217, *Suregada*.

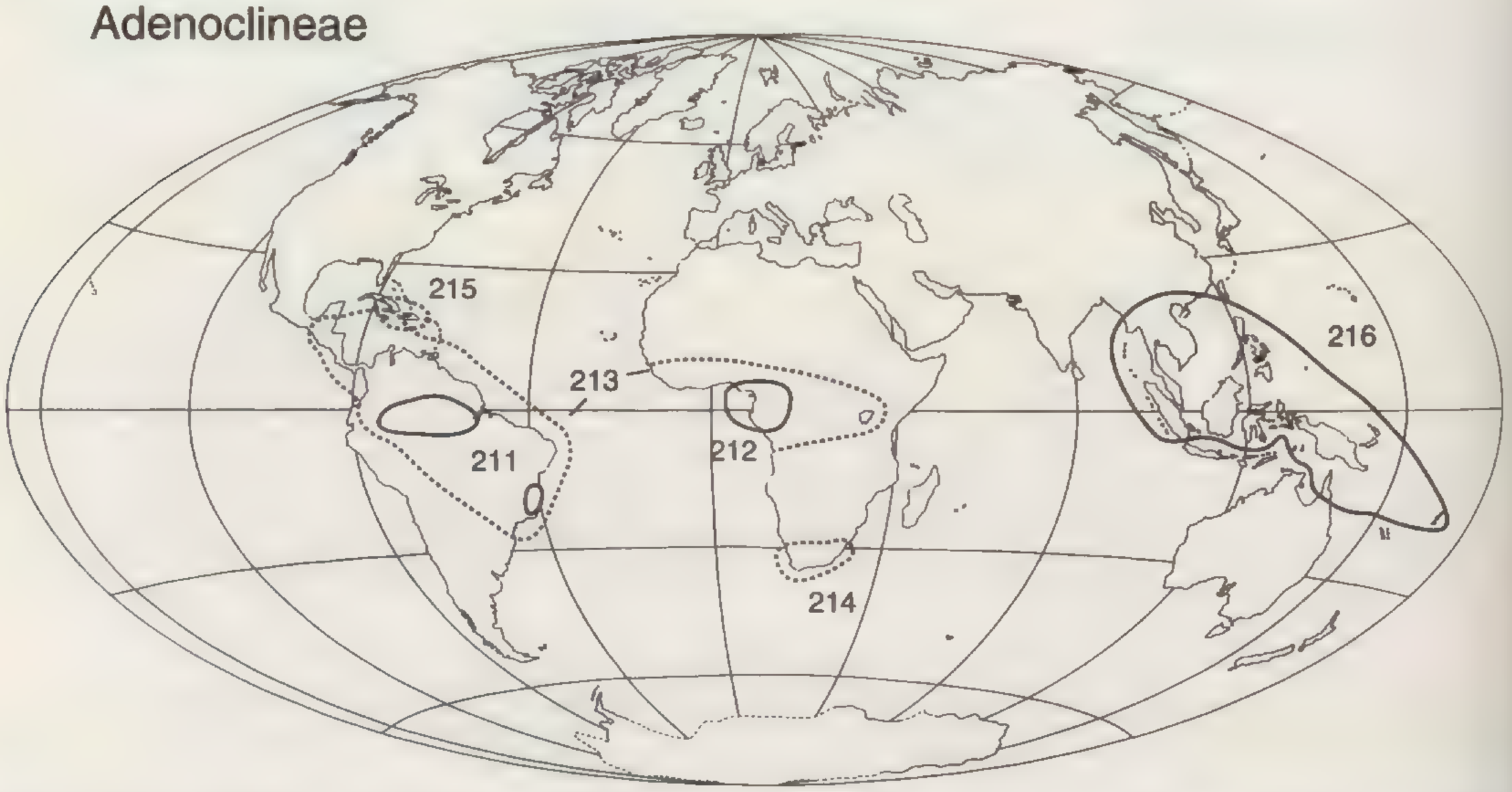

FIGURE 8.[3] Distribution of Crotonoideae, tribe Adenoclineae: 211, *Glycydendron* (solid line, America); 212, *Klaineanthus* (solid line, Africa); 213, *Tetrorchidium* (dashed line); 214, *Adenocline* (dotted line, Africa); 215, *Ditta* (dotted line, North America); 216, *Endospermum* (solid line, Asia & Australasia).

can be refined. It now appears that Africa/Madagascar retains the largest number of primitive taxa of Phyllanthoideae, and is the most likely center of origin for the family, but South America would seem to be the cockpit of initial differentiation for both the Oldfieldioideae and Crotonoideae. For both the Acalyphoideae and Euphorbioideae, the trail of clues leads back to a joint South American/African center, but a narrower designation of original locality must await further studies.

With regard to the role of long-distance dispersal in possibly accounting for these geographic pat-

FIGURE 9.[3] Distribution of Euphorbioideae, tribe Stomatocalyceae: 272, *Plagiostyles* (solid line, Africa); 273, *Pimelodendron* (solid line, Asia); 274, *Hamilcoa* (dotted line); 275, *Nealchornea* (solid line, America).

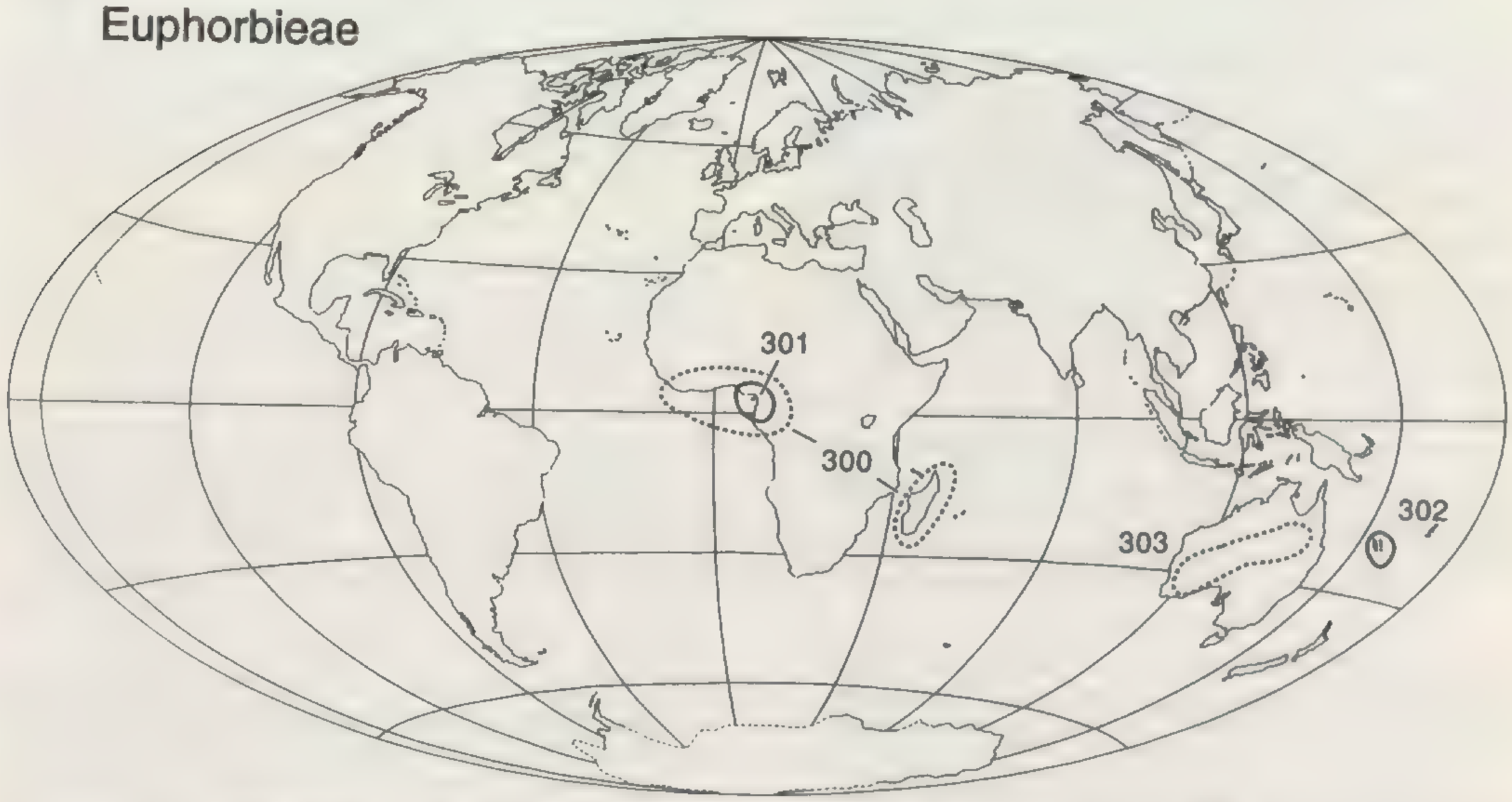

FIGURE 10.[3] Distribution of Euphorbioideae, tribe Euphorbieae. Subtribe Anthosteminae: 300, *Anthostema* (dashed line, Africa & Madagascar); 301, *Dichostemma* (solid line, Africa). Subtribe Neoguillauminiinae: 302, *Neoguillauminia* (solid line, New Caledonia); 303, *Calycopeplus* (dashed line, Australia).

terns, which Thorne (1972) and more recently Carlquist (1983) implied may be operative for many tropical intercontinental disjunctions, it is notable that the "basal" taxa in the Phyllanthoideae, Oldfieldioideae, and Acalyphoideae have capsular fruits with dry seed-coats, which certainly do not suggest a high degree of "preadaptation" for transoceanic dispersal. Only in the Adenoclineae of the Crotonoideae (Fig. 8) and the Stomatocalyceae of the Euphorbioideae (Fig. 9) do fleshy fruits or seeds occur that seem more likely to have been transported by birds. The weedy nature of many Euphorbiaceae would indeed appear to predispose them for success in establishment after transoceanic dispersal. However, the patterns reviewed above suggest that in the Euphorbiaceae, as in many other angiosperm families, the spectacular ocean crossings have been achieved by taxa (e.g., *Euphorbia*) that appear to have evolved later in family evolution, at a time when the continents were known to be widely separated. As suggested by Schuster (1976), the progressive refinement of dispersal capabilities during the course of the Tertiary leads to the paradox that the most widely dispersed genera are the latest evolved, and so the dramatic cases of long-distance transoceanic dispersal often noted in the literature tell us a great deal about the geologically recent stocking of oceanic islands but very little about the migrational history of less highly evolved taxa that were dispersing in the late Cretaceous or earliest Tertiary. Because of this paradox, Thorne (1973) appears correct in claiming that American/African disjuncts such as *Mayaca*, *Pitcairnia*, and *Saccoglottis* represent recent long-distance dispersal, but he goes too far in concluding that this explanation may be extended to all of the taxa that link America with Africa. The transoceanic vicariant patterns of genera and tribes in the Euphorbiaceae agree with those of many other tropical families mapped and discussed by Axelrod (1970, 1972, 1975); these strongly suggest that the differentiation of genera and tribes was decisively influenced by ocean-floor spreading.

There is a third alternative explanation for trans-Atlantic or trans-Pacific distributions in Euphorbiaceae, and that is overland migration at high latitudes during the early Tertiary; Wolfe (1972) proposed that some tropical groups crossed into America from Asia during the Eocene by the Bering land bridge. It is notable, however, that the genera he cited—*Meliosma*, *Sagaretia*, and *Saurauia*—are cloudforest rather than lowland tropical taxa; the suggested presence of Lecythidaceae and Myristicaceae is more significant, but requires confirmation. The distribution of Euphorbiaceae does not offer much support for this Beringian alternative migrational pathway. In the Phyllanthoideae, a possible example is *Flueggea* (Webster, 1984); however, this genus has also colonized Hawaii (Hayden, 1987). There are also possible trans-Pacific or trans-Atlantic links in the subtribe Antidesminae. The Oldfieldioideae show no indication of possible use

of the Alaskan corridor. In the Acalyphoideae and Crotonoideae, an intrusion from Asia into America is suggested by the Tertiary records of *Aleurites* and *Macaranga* (Wolfe & Leopold, 1967). There is little sign of this in living taxa, however; perhaps the best example is in Crotonoideae tribe Codiaeae, where the North American genus *Acidocroton* appears to be a vicariant of the Asian *Blachia*. In the Euphorbiaceae, therefore, an Eocene migration into America from Eurasia seems to have been an unimportant pathway. For explaining transoceanic links at the tribal level, a convincing model will have to involve plate tectonics as a major determinant.

Although the overall ecology of the Euphorbiaceae has not been reviewed in detail, it is worthwhile noting that genera of subfamily Phyllanthoideae with many plesiomorphic characters (e.g., *Heywoodia*, *Savia*) occur as shrubs or small trees in seasonal woodlands or scrub formations in the Southern Hemisphere. Except for the Acalyphoideae, the "basal" genera in the other subfamilies occur in rainforest or at least more mesic habitats; thus the spectacular efflorescence of xerophytes such as the African succulent Euphorbieae, *Jatropha*, and *Manihot*, appears to be a later development. In all five subfamilies, insect pollination is the plesiomorphic condition, and wind pollination has evolved independently within each subfamily. Relatively few Euphorbiaceae have become canopy trees in rainforest; rather, the family has specialized in an opportunistic life-style involving colonization of fragmented, shifting, or extreme (e.g., desert) habitats.

In closing this essay, I feel obliged to emphasize the large amount of conjecture that has been necessary in discussing the major patterns of tribal differentiation and continental deployment in the Euphorbiaceae. Perhaps we can keep our feet on the ground if we imagine our reconstructed phylogenies as a fireworks display: colorful, intricate, cleverly contrived, and evanescent. There may be a correspondence here between the mental activity of the systematist and the master-plan of evolution: if we allow the rockets to represent family ancestors (or plesiomorphic states), and their trajectory the onward rush in evolutionary time, then the first burst of the rocket's red glare will represent the formations of tribes, subsequent pops genera, and the final transient fizzles, the species. The sedate appearance of cladograms in our scholarly papers represents an austere, abstract schematization of the turbulent, convoluted, and ultimately partly unknowable history of the Euphorbiaceae and other plant taxa.

Literature Cited

Airy Shaw, H. K. 1972. The Euphorbiaceae of Siam. Kew Bull. 26: 191–363.

———. 1975. The Euphorbiaceae of Borneo. Kew Bull. Add. Ser. 4: 1–245.

———. 1980. The Euphorbiaceae of New Guinea. Kew Bull. Add. Ser. 8: 1–253.

Alex, A. H. 1957. Pollination of some oil seed crops by honey bees. Texas A. & M. Coll. Agr. Exp. Sta. Progr. Rep. 1960.

Anton, R. 1974. Etude chimiotaxonomique sur le genre *Euphorbia* (Euphorbiacées). Thèse, Université Louis Pasteur, Strasbourg.

Armbruster, W. S. 1982. Seed production and dispersal in *Dalechampia* (Euphorbiaceae): Divergent patterns and ecological consequences. Amer. J. Bot. 69: 1429–1440.

———. 1984. The role of resin in angiosperm pollination: Ecological and chemical considerations. Amer. J. Bot. 71: 1141–1160.

———. 1988. Multilevel comparative analysis of the morphology, function, and evolution of *Dalechampia* (Euphorbiaceae) blossoms. Ecology 69: 1746–1761.

———. 1992. Phylogeny and the evolution of plant-animal interactions. BioScience 42: 12–20.

——— & A. L. Herzig. 1984. Partitioning and sharing of pollinators by four sympatric species of *Dalechampia* (Euphorbiaceae) in Panama. Ann. Missouri Bot. Gard. 71: 1–16.

——— & G. L. Webster. 1979. Pollination of two species of *Dalechampia* (Euphorbiaceae) in Mexico by euglossine bees. Biotropica 11: 278–283.

Axelrod, D. I. 1970. Mesozoic paleogeography and early angiosperm history. Bot. Rev. 36: 277–319.

———. 1972. Ocean-floor spreading in relation to ecosystematic problems. *In:* R. T. Allen & F. C. James (editors), A Symposium on Ecosystematics. Univ. Ark. Mus. Occ. Pap. 4: 15–68.

———. 1975. Plate tectonics and problems of angiosperm history. Mém. Mus. Nat. Hist. Nat. II. 88A: 72–86.

Baillon, H. 1858. Etude Générale du Groupe des Euphorbiacées. Victor Masson, Paris.

———. 1873. Nouvelles observations sur les Euphorbiacées. Adansonia I. 11: 72–138.

Bally, P. R. O. 1961. The genus *Monadenium*. Benteli, Berne.

Bamber, R. K. 1974. Fibre types in woods of Euphorbiaceae. Austral. J. Bot. 22: 629–634.

Bancilhon, L. 1971. Contribution à l'étude taxonomique du genre *Phyllanthus* (Euphorbiacées). Boissiera 18: 1–81.

Bawa, K. S. 1980. Evolution of dioecy in flowering plants. Ann. Rev. Ecol. Syst. 11: 15–39.

Belin-Depoux, M. 1977. Introduction à l'étude des glandes foliaires de l'*Alchornea cordata* (Juss.) Muell. Arg. (Euphorbiaceae). Rev. Gén. Bot. 84: 127–136.

——— & D. Clair-Maczulajtys. 1974. Introduction à l'étude des glandes foliaires de l'*Aleurites moluccana* Willd. (Euphorbiacée) I. La glande et son ontogenèse. Rev. Gén. Bot. 81: 335–351.

——— & ———. 1975. Introduction à l'étude des glandes foliaires de l'*Aleurites moluccana* Willd. (Euphorbiacée) II. Aspects histologiques et cytologiques de la glande pétiolaire fonctionelle. Rev. Gén. Bot. 82: 119–155.

BENTHAM, G. 1878. Notes on Euphorbiaceae. J. Linn. Soc. London, Bot. 17: 185–267.

———. 1880. Euphorbiaceae. *In:* G. Bentham & J. D. Hooker (editors), Gen. Pl. 3: 239–340.

BERG, R. 1975a. Myrmecochorous plants in Australia and their dispersal by ants. Austral. J. Bot. 23: 475–508.

———. 1975b. Fruit, seed, and myrmecochorous dispersal in *Micrantheum* (Euphorbiaceae). Norwegian J. Bot. 22: 173–194.

———. 1981. The role of ants in seed dispersal in Australian lowland heathland. Pp. 51–59 *in* R. L. Specht (editor), Heathlands and Related Shrublands: Analytical Studies [Ecosystems of the World 9B]. Elsevier, Amsterdam.

BERNHARD, F. 1966. Contribution à l'étude des glandes foliaires chez les Crotonoidées (Euphorbiacées). Mém. Inst. Fond. Afr. Noire 75: 71–156.

BOR, J. & R. N. KAPIL. 1976. Anatropy and ontogeny of the bitegmic ovule in *Chrozophora* A. H. L. Jussieu (Euphorbiaceae). Acta Bot. Neerl. 25: 385–400.

BRECKON, G. 1975. *Cnidoscolus*, Section *Calyptosolen* (Euphorbiaceae) in Mexico and Central America. Ph.D. Dissertation Title. University of California, Davis.

BRESINSKY, A. 1963. Bau, Entwicklungsgeschichte und Inhaltsstoffe der Elaiosomen. Bibl. Bot. 126: 1–54.

BULLOCK, S. H. 1982. Componentes fenológicos del sistema de cruzamiento monóico de *Cnidoscolus spinosus* (Euphorbiaceae) en Jalisco. Bol. Soc. Bot. Mex. 42: 1–9.

CARANO, E. 1926. Ulteriori osservazioni su *Euphorbia dulcis* L. in rapporto col suo comportamento apomittico. Ann. Bot. Roma 17: 50–79.

CARLQUIST, S. 1970. Wood anatomy of Hawaiian, Macronesian and other species of *Euphorbia*. Bot. J. Linn. Soc. 63 (suppl.): 181–193.

———. 1983. Intercontinental dispersal. Sonderbd. naturwiss. Ver. Hamburg 7: 37–47.

CESCA, G. 1961. Ricerche cariologiche ed embriologiche sulle Euphorbiaceae. I—su alcuni biotipi di *Euphorbia dulcis* L. della Toscana. Caryologia 14: 79–96.

———. 1969. Cytological and embryological studies in the genus *Euphorbia*: *Euphorbia epithymoides* L. Proc. Natl. Inst. Sci. India (Nat.) 35: 139–152.

COOK, A. D., P. R. ATSATT & C. A. SIMON. 1971. Doves and dove weed: Multiple defenses against avian predation. Bioscience 21: 277–281.

CORNER, E. J. H. 1976. The Seeds of Dicotyledons. 2 vols. Cambridge Univ. Press, Cambridge.

CREMERS, G. 1977. Architecture végétative de quelques espèces malgaches du genre *Euphorbia* L. Bull. Jard. Bot. Nat. Belg. 47: 55–81.

CREPET, W. L. & C. P. DAGLIAN. 1982. Euphorbioid inflorescences from the Middle Eocene Claiborne formation. Amer. J. Bot. 69: 258–266.

CROIZAT, L. 1943. New or critical Euphorbiaceae of Brazil. Trop. Woods 76: 11–14.

———. 1972. An introduction to the subgeneric classification of *Euphorbia* L. with stress on the South African and Malagasy species. III. Webbia 27: 1–221.

CRONQUIST, A. 1981. An Integrated System of Classification of Flowering Plants. Columbia Univ. Press, New York.

DAUMANN, E. 1972. Zur Blütenmorphologie und Bestäubungsökologie von *Mercurialis* L. Preslia 44: 308–315.

DAVIS, G. 1966. Systematic Embryology of Angiosperms. Wiley & Sons, New York.

DEHAY, C. 1935. L'appareil libero-ligneux foliare des Euphorbiacées. Ann. Sci. Nat. Bot. X. 17: 147–190.

DEHGAN, B. 1980. Application of epidermal morphology to taxonomic delimitations in the genus *Jatropha* L. (Euphorbiaceae). Bot. J. Linn. Soc. 80: 257–278.

———. 1982. Comparative anatomy of the petiole and infrageneric relationships in *Jatropha* (Euphorbiaceae). Amer. J. Bot. 69: 1283–1295.

——— & M. E. CRAIG. 1978. Types of laticifers and crystals in *Jatropha* and their taxonomic implications. Amer. J. Bot. 65: 345–352.

——— & G. L. WEBSTER. 1979. Morphology and infrageneric relationships of the genus *Jatropha* (Euphorbiaceae). Univ. Calif. Publ. Bot. 74: 1–73.

DILCHER, D. L. & S. R. MANCHESTER. 1988. Investigations of angiosperms from the Eocene of North America: A fruit belonging to the Euphorbiaceae. Tertiary Res. 9: 45–58.

DINGLER, H. 1885. Die Flachsprosse der Phanerogamen. Erstes Heft: *Phyllanthus* sect. *Xylophylla*. T. Ackermann, Munich.

DOMINGUEZ, C. A. & S. H. BULLOCK. 1989. La reproducción de *Croton suberosus* (Euphorbiaceae) en luz y sombra. Rev. Biol. Trop. 37: 1–10.

———, R. DIRZO & S. H. BULLOCK. 1989. On the function of floral nectar in *Croton suberosus* (Euphorbiaceae). Oikos 56: 109–114.

DRESSLER, R. L. 1957. The genus *Pedilanthus* (Euphorbiaceae). Contr. Gray Herb. 182: 1–188.

EHRENFELD, J. 1976. Reproductive biology of three species of *Euphorbia* subgenus *Chamaesyce* (Euphorbiaceae). Amer. J. Bot. 63: 406–413.

EICHLER, A. W. 1875. Blütendiagramme. Wilhelm Engelmann, Leipzig.

ERDTMAN, G. 1952. Pollen Morphology and Plant Taxonomy. Almqvist & Wiksells, Uppsala.

FROEMBLING, W. 1896. Anatomische-systematische Untersuchung von Blatt und Axe der Crotoneen und Euphyllantheen. Inaug.-Dissert., Gebr. Gotthelft, Cassel.

GAUCHER, L. 1902. Recherches anatomiques sur les Euphorbiacées. Ann. Sci. Nat. Bot. 15: 161–309.

GIBBS, 1974. Chemotaxonomy of Flowering Plants. 4 vols. McGill-Queen's Univ. Press, Montreal & London.

GILBERT, M. G. 1994. The relationships of the Euphorbieae. Ann. Missouri Bot. Gard. 81: 283–288.

GIVNISH, T. J. 1982. Outcrossing versus ecological constraints in the evolution of dioecy. Amer. Nat. 119: 849–865.

GOTTSBERGER, G. 1978. Seed dispersal by fish in the inundated regions of Humaitá, Amazonia. Biotropica 10: 170–183.

HALLE, F. 1971. Architecture and growth of tropical trees exemplified by the Euphorbiaceae. Biotropica 3: 56–62.

——— & R. A. OLDEMAN. 1970. Essai sur l'architecture et la dynamique de croissance des arbres tropicaux. Masson, Paris.

———, R. A. OLDEMAN & P. B. TOMLINSON. 1978. Tropical Trees and Forests: An Architectural Analysis. Springer Verlag, Heidelberg.

HANS, A. S. 1973. Chromosomal conspectus of the Euphorbiaceae. Taxon 22: 591–636.

HAUMAN-MERCK, L. 1912. Observations d'éthologie florale sur quelques espèces argentines et chiliennes. Rec. Inst. Bot. Léo Errera 9: 3–20.

HAYDEN, W. J. 1977. Comparative anatomy and systematics of *Picrodendron*, genus *Incertae sedis*. J. Arnold Arb. 58: 257–279.

———. 1980. Systematic Anatomy of Oldfieldioideae (Euphorbiaceae). Doctoral Dissertation Title, University of Maryland.

———. 1987. The identity of the genus *Neowawraea* (Euphorbiaceae). Brittonia 39: 268–277.

———. 1988. Ontogeny of the cotyledonary region of *Chamaesyce maculata* (Euphorbiaceae). Amer. J. Bot. 75: 1701–1713.

———, W. T. GILLIS, D. E. STONE, C. R. BROOME & G. L. WEBSTER. 1984. Systematics and palynology of *Picrodendron*: Further evidence for relationship with the Oldfieldioideae (Euphorbiaceae). J. Arnold Arbor. 65: 105–127.

HEGNAUER, R. 1962–73. Chemotaxonomie der Pflanzen: Eine Übersicht über die Verbreitung und der Systematische Bedeutung der Pflanzenstoffe. 6 vols. Birkhauser, Basel.

HERBERT, H. 1897. Anatomische Untersuchung von Blatt und Axe der Hippomaneen. Inaug.-Diss., Munich.

HICKEY, L. J. & J. A. WOLFE. 1975. The bases of angiosperm phylogeny: Vegetative morphology. Ann. Missouri Bot. Gard. 62: 538–589.

HURUSAWA, I. 1954. Eine nochmalige Durchsicht des herkömmlichen Systems der Euphorbiaceen im weiteren Sinne. J. Fac. Sci. Univ. Tokyo, Bot. 6: 209–342.

HUTCHINSON, J. 1969. Tribalism in the family Euphorbiaceae. Amer. J. Bot. 56: 738–758.

INAMDAR, J. A. & M. GANGADHARA. 1977. Studies on the trichomes of some Euphorbiaceae. Feddes Repert. 88: 103–111.

JANSSONIUS, H. H. 1929. A contribution to the natural classification of the Euphorbiaceae. Trop. Woods 19: 8–11.

———. 1930. Mikrographie des Holzes der auf Java vorkommenden Baumarten [Euphorbiaceae, pp. 442–835]. Brill, Leiden.

JENSEN, U., I VOGEL-BAUER & M. NITSCHE. 1994. Leguminlike proteins and the systematics of the Euphorbiaceae. Ann. Missouri Bot. Gard. 81: 160–179.

JONES, K. & J. B. SMITH. 1969. The chromosome identity of *Monadenium* Pax and *Synadenium* Pax (Euphorbiaceae). Kew Bull. 23: 491–493.

JOSE, T. & J. A. INAMDAR. 1989. Structure, ontogeny and biology of nectaries in *Croton bonplandianus* Bail. Beitr. Biol. Pflanzen 64: 157–165.

JURY, S. L., T. REYNOLDS, D. F. CUTLER & F. J. EVANS (editors). 1987. The Euphorbiales: Chemistry, taxonomic & economic botany. Bot. J. Linn. Soc. 94: 1–326.

JUSSIEU, A. 1824. De Euphorbiacearum generibus medicisque earumdem viribus tentamen. Paris.

KAKKAR, L. & G. S. PALIWAL. 1974. Studies on the leaf anatomy of *Euphorbia* L. Epidermis. Proc. Indian Nat. Sci. Acad. 40B: 55–67.

KAPIL, R. N. 1961. Some embryological aspects of *Euphorbia dulcis* L. Phytomorphology 11: 24–36.

——— & A. K. BHATNAGAR. 1980. Embryology in relation to angiosperm taxonomy. Pp. 272–295 *in* P. K. K. Nair. (editor), Glimpses in Plant Research, vol. 5. Vikas Publ. House, New Delhi.

KNOLL, F. 1905. Die Brennhaare der Euphorbiaceen-Gattungen *Dalechampia* und *Tragia*. Sitzungsber. Kaiserl. Akad. Wiss. Math.-Nat. Klasse 114: 29–48.

KÖHLER, E. 1965. Die Pollenmorphologie der Biovulaten Euphorbiaceae und ihre Bedeutung für die Taxonomie. Grana Palynol. 6: 26–120.

LEACH, L. C. 1976. Distributional and morphological studies of the tribe Euphorbieae (Euphorbiaceae) and their relevance to its classification and possible evolution. Excelsa 6: 3–19.

LÉONARD, J. 1962. Euphorbiaceae. Fl. Congo 8(1): 1–214.

——— & M. MOSANGO. 1985. Hymenocardiaceae. Flore d'Afrique Centrale: Spermatophytes.

LEOPOLD, E. B. & H. D. MCGINITIE. 1972. Development and affinities of Tertiary floras in the Rocky Mountains. Pp. 147–200 *in* A. Graham (editor), Floristics and Paleofloristics of Asia and Eastern North America. Elsevier, Amsterdam.

LEROY, J.-F. 1976. Recherches sur la nature et l'origine de la fleur angiospermienne: Interprétation des structures dans un groupe singulier d'Euphorbiaceae. Compt. Rend. Hebd. Séances Acad. Sci., Sér. D. 283: 247–250.

LEVIN, G. A. 1986a. Systematic foliar morphology of Phyllanthoideae (Euphorbiaceae), I. Conspectus. Ann. Missouri Bot. Gard. 73: 29–85.

———. 1986b. Systematic foliar morphology of Phyllanthoideae (Euphorbiaceae). II. Phenetic analysis. Ann. Missouri Bot. Gard. 73: 86–98.

———. 1986c. Systematic foliar morphology of Phyllanthoideae III. Cladistic analysis. Syst. Bot. 11: 515–530.

——— & M. G. SIMPSON. 1994a. Phylogenetic implications of pollen ultrastructure in the Oldfieldioideae (Euphorbiaceae). Ann. Missouri Bot. Gard. 81: 203–238.

——— & M. G. SIMPSON. 1994b. Phylogenetic relationships of *Didymocistus* and *Hymenocardia* (Euphorbiaceae). Ann. Missouri Bot. Gard. 81: 239–244.

MAHESHWARI, P. 1942. The embryo-sac of *Euphorbia heterophylla* L.—A reinvestigation. Proc. Indian Acad. Sci. 15B: 158–166.

MAHLBERG, P. G. 1975. Evolution of the laticifer in *Euphorbia* as interpreted from starch grain morphology. Amer. J. Bot. 62: 577–583.

———, D. G. DAVIS, D. S. GALITZ & G. D. MANNERS. 1987. Laticifers and the classification of *Euphorbia*: The chemotaxonomy of *Euphorbia esula* L. Bot. J. Linn. Soc. 94: 165–180.

MARTIN, H. A. 1974. The identification of some Tertiary pollen belonging to the family Euphorbiaceae. Austral. J. Bot. 22: 271–291.

———. 1978. Evolution of the Australian flora and vegetation through the Tertiary: Evidence from pollen. Alcheringa 2: 181–202.

MAZER, S. J. & B. H. TIFFNEY. 1982. Fruits of *Wetherellia* and *Palaeowetherellia* (?Euphorbiaceae) from Eocene sediments in Virginia and Maryland. Brittonia 34: 300–333.

MEEUSE, A. D. J. 1990. The Euphorbiaceae auct. plur.: An unnatural taxon. Eburon, Delft.

MENNEGA, A. M. W. 1987. Wood anatomy of the Euphorbiaceae, in particular of the subfamily Phyllanthoideae. Bot. J. Linn. Soc. 94: 111–126.

METCALFE, C. R. & L. CHALK. 1950. Anatomy of the Dicotyledons. Clarendon Press, Oxford.

MICHAELIS, P. 1924. Blütenmorphologische Untersuchungen an den Euphorbiaceen. Bot. Abh. Jena 3: 1–150.

MILLER, K. & G. L. WEBSTER. 1962. Systematic position of *Cnidoscolus* and *Jatropha*. Brittonia 14: 174–180.

MOLDENKE, A. R. 1976. California pollination ecology and vegetation types. Phytologia 34: 305–361.

MUELLER, J. 1866. Euphorbiaceae. DC. Prodr. 15(2): 189–1261.

———. 1874. Euphorbiaceae [part 2]. *In:* Martius, Fl. Bras. 11(2): 293–750.

NETOLITZKY, F. 1926. Anatomie der Angiospermen-Samen. Gebrüder Borntraeger, Berlin.

NOWICKE, J. W. 1994. A palynological study of Crotonoideae (Euphorbiaceae). Ann. Missouri Bot. Gard. 81: 245–269.

NOZERAN, R. 1953. Sur quelques fleurs males d'Euphorbiacées. Rec. Trav. Lab. Bot. Univ. Montpellier Bot. 6: 99–114.

PAX, F. 1884. Die Anatomie der Euphorbiaceen in ihrer Beziehung zum System derselben. Bot. Jahrb. 5: 384–421.

———. 1890. Euphorbiaceae. *In:* A. Engler & K. Prantl (editors), Die Natürl. Pflanzenfam. ed. 1, 3(5): 1–119.

———. 1910. Euphorbiaceae–Jatropheae. *In* A. Engler (editor), Das Pflanzenreich IV. 147. I (Heft 42): 1–148.

———. 1924. Die Phylogenie der Euphorbiaceae. Bot. Jahrb. 59: 129–184.

——— & K. HOFFMANN. 1931. Euphorbiaceae. *In* A. Engler & K. Prantl (editors), Die Natürl. Pflanzenfam. ed. 2, 19c: 11–233.

PERKINS, G., J. R. ESTES & R. W. THORP. 1975. Pollination of *Cnidoscolus texanus* (Euphorbiaceae) in south-central Oklahoma. Southw. Nat. 20: 391–396.

PERRY, B. 1943. Chromosome number and phylogenetic relationships in the Euphorbiaceae. Amer. J. Bot. 30: 527–543.

PIJL, L. VAN DER. 1952. The stamens of *Ricinus*. Phytomorphology 2: 130–132.

———. 1982. Principles of Dispersal in Higher Plants, 3rd ed. Springer-Verlag, Berlin.

PUNT, W. 1962. Pollen morphology of the Euphorbiaceae with special reference to taxonomy. Wentia 7: 1–116.

———. 1987. A survey of pollen morphology in Euphorbiaceae with special reference to *Phyllanthus*. Bot. J. Linn. Soc. 94: 127–142.

RADCLIFFE-SMITH, A. 1987. Segregate families from the Euphorbiaceae. Bot. J. Linn. Soc. 94: 47–66.

RADLKOFER, L. 1870. Ueber *Pausandra*, ein neues Euphorbiaceen-Genus. Flora 53: 81–95.

RAJU, V. S. & P. N. RAO. 1977. Variation in the structure and development of foliar stomata in the Euphorbiaceae. Bot. J. Linn. Soc. 75: 69–97.

——— & ———. 1987. The taxonomic use of the basal stomatal type in the generic delimitation of *Chamaesyce* (Euphorbiaceae). Feddes Repert. 98: 137–141.

RAO, A. R. 1970. Euphorbiaceae. *In:* Proceedings of the Symposium on Comparative Embryology of the Angiosperms. Bull. Indian Nat. Sci. Acad. 41: 136–141.

RAO, A. R. & M. MALAVIYA. 1964. On the latex-cells and latex of *Jatropha*. Proc. Indian Acad. Sci. 60B: 95–106.

RAO, P. R. & V. S. RAJU. 1985. Foliar trichomes in the family Euphorbiaceae. Pp. 128–136 *in* B. Singh & M. P. Singh (editors), Trends in Plant Research. Govil & Kumar, Dehra Dun.

RAVEN, P. H. & D. J. AXELROD. 1974. Angiosperm biogeography and past continental movements. Ann. Missouri Bot. Gard. 61: 539–673.

REDDI, E. U. B. & C. S. REDDI. 1983. Pollination ecology of *Jatropha gossypiifolia* (Euphorbiaceae). Proc. Indian Acad. Sci. (Plant Sci.) 92: 215-231.

RITTERSHAUSEN, P. 1892. Anatomisch-systematische Untersuchung von Blatt und Axe der Acalypheen. Inaug.-Dissert,. Munich.

ROSSIGNOL, L. & M. ROSSIGNOL. 1985. Architecture et tendances évolutives dans le genre *Phyllanthus* (Euphorbiaceae). Bull. Mus. Nat. Hist. Nat. IV. 7: 67–80.

ROTHDAUSCHER, H. 1896. Ueber die anatomischen Verhaltnisse von Blatt und Axe der Phyllantheen (mit Auschluss der Euphyllantheen). Inaug.-Dissert., Cassel (also published in Bot. Centrabl. 68).

ROUX, J. 1968. Sur le comportement des axes aériens chez quelques plantes à rameaux végétatifs polymorphes; le concept de rameaux plagitropes. Ann. Sci. Nat. Bot. XII. 9: 109–256.

RUDALL, P. J. 1987. Laticifers in Euphorbiaceae—A conspectus. Bot. J. Linn. Soc. 94: 143–163.

SCHUSTER, R. M. 1976. Plate tectonics and its bearing on the geographical origin and dispersal of angiosperms. Pp. 48–138 *in* C. B. Beck (editor), Origin and Early Evolution of Angiosperms. Columbia Univ. Press, New York.

SCHWEIGER, J. 1905. Beitrage zur Kenntnis der Samenentwicklung der Euphorbiaceen. Flora. 94: 339–379.

SEHGAL, L. & G. S. PALIWAL. 1974. Studies on the leaf anatomy of *Euphorbia*—VIII. General conclusions and systematic considerations. Phytomorphology 24: 141–151.

SIMPSON, B. B. 1977. Breeding systems of dominant perennial plants of two disjunct warm desert ecosystems. Oecologia 27: 203–226.

SINGH, R. P. 1962. Forms of ovules in Euphorbiaceae. Pp. 124–128 *in* Plant Embryology, A Symposium. New Delhi.

SMITH, J. 1841. Notice of a plant which produces perfect seeds without any apparent action of pollen on the stigma. Trans. Linn. Soc. London 18: 512.

SNOW, D. W. 1981. Tropical frugivorous birds and their food plants: A world survey. Biotropica 13: 1–14.

SOLEREDER, H. 1899. Systematische Anatomie der Dicotyledonen. Enke, Stuttgart.

———. 1908. Systematische Anatomie der Dicotyledonen. Ergänzungsband. Enke, Stuttgart.

STEINER, K. E. 1981. Nectarivory and potential pollination by a Neotropical marsupial. Ann. Missouri Bot. Gard. 68: 505–513.

———. 1982. Mistake Pollination of *Hura crepitans* (Euphorbiaceae) by Frugivorous Bats. Doctoral Dissertation Title. University of California, Davis.

———. 1983. Pollination of *Mabea occidentalis* (Euphorbiaceae) in Panama. Syst. Bot. 8: 105–117.
———. 1988. Dioecism and its correlates in the Cape flora of South Africa. Amer. J. Bot. 75: 1742–1754.
TAYLOR, D. W. 1990. Paleobiogeographic relationships of angiosperms from the Cretaceous and early Tertiary of the North American area. Bot. Rev. 56: 279–417.
THORNE, R. F. 1972. Major disjunctions in the geographic ranges of seed plants. Quart. Rev. Biol. 47: 365–411.
———. 1973. Floristic relationships between tropical Africa and tropical America. Pp. 27–47 *in* B. J. Meggers et al. (editors), Tropical Forest Ecosystems in Africa and South America: A Comparative Review. Smithsonian Institution, Washington.
THURSTON, E. L. 1976. Morphology, fine structure and ontogeny of the stinging emergences of *Tragia ramosa* and *T. saxicola* (Euphorbiaceae). Amer. J. Bot. 63: 710–718.
——— & N. R. LERSTEN. 1969. The morphology and toxicology of plant stinging hairs. Bot. Review 35: 393–412.
UHLARZ, H. 1978. Ueber die Stipularorgane der Euphorbiaceae, unter besonderer Berucksichtigung ihrer Rudimentation. Trop. Subtrop. Pflanzenwelt. 23: 1–65.
URBATSCH, L. E., J. D. BACON, R. L. HARTMAN, M. C. JOHNSTON, T. J. WATSON JR. & G. L. WEBSTER. 1975. Chromosome numbers for North American Euphorbiaceae. Amer. J. Bot. 62: 494–500.
VENKATA RAO, C. 1971. Anatomy of the inflorescence of some Euphorbiaceae. Bot. Not. 124: 39–64.
———. 1972. Floral anatomy of *Ricinocarpus pinifolius* with some observations on the phylogeny and centre of origin of Euphorbiaceae. Adv. Pl. Morphol. 1972: 85–91.
——— & T. RAMALAKSHMI. 1968. Floral anatomy of the Euphorbiaceae—I. Some non-cyathium taxa. J. Indian Bot. Soc. 47: 278–300.
VINDT, J. 1960. Monographie des Euphorbiacées du Maroc. Deuxième partie: Anatomy. Trav. Inst. Sci. Chérifien, Bot. 19: 219–533.
VOGEL, C. 1986. Phytoserologische Untersuchungen zur Systematik der Euphorbiaceae; Beitrage zur infrafamiliaren Gliederung und zu Beziehungen im extrafamiliaren Bereich. Dissert. Bot. 98: 1–124.
WARMKE, H. E. 1952. Studies on natural pollination of *Hevea brasiliensis* in Brazil. Science 116: 474–475.
WEBSTER, G. L. 1956. A monographic study of the West Indian species of *Phyllanthus*. J. Arnold Arbor. 37: 91–122, 217–268, 340–359.
———. 1957. A monographic study of the West Indian species of *Phyllanthus*. J. Arnold Arbor. 38: 51–80, 170–198, 295–373.
———. 1958. A monographic study of the West Indian species of *Phyllanthus*. J. Arnold Arbor. 39: 49–100, 111–212.
———. 1967. The genera of Euphorbiaceae in the southeastern United States. J. Arnold Arbor. 48: 303–430.
———. 1975. Conspectus of a new classification of the Euphorbiaceae. Taxon 24: 593–601.
———. 1979. A revision of *Margaritaria* (Euphorbiaceae). J. Arnold Arbor. 60: 403–444.
———. 1984. A revision of *Flueggea* (Euphorbiaceae). Allertonia 3: 259–312.
———. 1987. The saga of the spurges: A review of classification and relationships of the Euphorbiales. Bot. J. Linn. Soc. 94: 3–46.
———. 1994. Synopsis of the genera and suprageneric taxa of Euphorbiaceae. Ann. Missouri Bot. Gard. 81: 33–144.
——— & K. MILLER. 1963. The genus *Reverchonia* (Euphorbiaceae). Rhodora 65: 193–207.
——— & E. RUPERT. 1973. Phylogenetic significance of pollen nuclear number in the Euphorbiaceae. Evolution 27: 524–531.
——— & B. D. WEBSTER. 1972. The morphology and relationships of *Dalechampia scandens* (Euphorbiaceae). Amer. J. Bot. 59: 573–586.
———, W. V. BROWN & B. N. SMITH. 1975. Systematics of photosynthetic carbon fixation pathways in *Euphorbia*. Taxon 24: 27–33.
———, E. RUPERT & D. KOUTNIK. 1982. Systematic significance of pollen nuclear number in Euphorbiaceae, tribe Euphorbieae. Amer. J. Bot. 69: 407–415.
WOLFE, J. A. 1972. An interpretation of Alaskan Tertiary floras. Pp. 201–233 *in* A. Graham (editor), Floristics and Paleofloristics of Asia and Eastern North America. Elsevier, Amsterdam.
———. 1975. Some aspects of plant geography of the Northern Hemisphere during the late Cretaceous and Tertiary. Ann. Missouri Bot. Gard. 62: 264–279.
WOLFE, J. A. & E. B. LEOPOLD. 1967. Neogene and early Quaternary vegetation of northwestern North America and northeastern Asia. Pp. 193–206 *in* D. M. Hopkins (editor), The Bering Land Bridge. Stanford Univ. Press, Stanford.
WUNDERLICH, R. 1968. Some remarks on the taxonomic significance of the seed coat. Phytomorphology 17: 301–311.

SYNOPSIS OF THE GENERA AND SUPRAGENERIC TAXA OF EUPHORBIACEAE[1]

Grady L. Webster[2]

ABSTRACT

This revised synopsis of the taxa of Euphorbiaceae recognizes, and provides keys to, 5 subfamilies, 49 tribes, and 317 genera. Two new tribes, Croizatieae and Podocalyceae, are proposed, as well as four new subtribes, Leptopinae, Podocalycinae, Pycnocominae, and Tetracoccinae; five taxa are reduced to subtribal status. One genus (*Ophellantha*) is reduced to a section; 14 new binomial combinations are proposed. Lectotypifications are provided for almost all taxa not previously typified.

The synoptic classification given here provides keys to and descriptions of the taxa of Euphorbiaceae at the subfamilial, tribal, and subtribal levels. It represents an extension and, in places, a considerable revision of the synoptic classification in which the five subfamilies were first recognized (Webster, 1975). Within the tribes and subtribes, keys are provided to the genera, and these are enumerated with citation of important synonyms. Keys are intended to provide the salient diagnostic characters of taxa, but do not necessarily allow for exceptions; in some instances, they may be of limited use in identifying unknown specimens to genus. Citations of synonyms and relevant works have been deliberately kept brief and are not intended to be all-inclusive; by and large, only strictly systematic papers are cited. Some obscure synonyms, including most of the names proposed by Rafinesque and Otto Kuntze, have been omitted. Typifications follow *Index Nominum Genericorum* (Farr et al., 1979); new typifications or alterations of entries in *ING* are explicitly noted. Generic concepts are relatively conservative; i.e., traditional usage is followed where possible. In borderline cases, genera are enumerated as distinct even though their claim to generic status may be questionable; listing of taxa here is therefore not intended to be canonical. A list of new taxa and an index to the genera and higher taxa are given in the appendices to this article.

Euphorbiaceae A. L. de Jussieu, Gen. Pl. 384. 1789. TYPE: *Euphorbia* L.

Monoecious or dioecious trees, shrubs, or herbs (some climbing or twining); stems sometimes succulent and/or with latex. Leaves alternate or opposite (rarely whorled); stipules free (less commonly connate or absent), deciduous or persistent; leaf blades pinnately or palmately veined, entire to dentate or palmately lobed or compound; indumentum simple to stellate or lepidote (sometimes absent). Inflorescences terminal or axillary, basically cymose; flowers solitary or in glomerules, these often grouped into spiciform or capitate thyrses or pseudanthia; bracts often glandular. Flowers unisexual, actinomorphic (but pseudanthia often zygomorphic); perianth segments free or connate, valvate or imbricate, sometimes reduced or absent; sepals and petals (1–)3–6(–8), sometimes distinctly colored; disk present or absent, intrastaminal or extrastaminal, entire to dissected; stamens (1–)3–50(–400) [always 1 in *Euphorbia*], hypogynous; filaments free or connate; anthers mostly 2-locular and dehiscing longitudinally, introrse or extrorse; pollen grains tectate or semi-tectate, mostly 3-colporate (inaperturate to polytreme); gynoecium syncarpous, ovary (1–)2–5(–20)-locular; placentation axile; ovules 1 or 2 per locule, anatropous or hemitropous (orthotropous in *Panda*), inserted beneath an obturator, crassinucellate with 2 integ-

[1] I express my gratitude to John Hayden and Geoffrey Levin for reviewing the treatment of the Oldfieldioideae, Lynn Gillespie for tribe Plukenetieae, and Daryl Koutnik for tribe Euphorbieae. Their suggestions have led to some important modifications in circumscriptions and interpretations of taxa. I am also particularly indebted to Michael Huft and Geoffrey Levin for their critical reviews of the manuscript, to Geoffrey Levin for compiling the index, and to Robert Rhode for help in formatting the text.

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uments, nucellus often beaked, embryo sac mostly 8-nucleate; styles free or connate, entire to lobed or multifid. Fruit typically a capsular schizocarp with mericarps elastically dehiscent from a persistent columella, but sometimes baccate or drupaceous; seeds 1 or 2 per locule (rarely 1 per fruit); seed coat thin to indurate, sometimes with a sarcotesta; endosperm present or absent; embryo straight to curved or folded; cotyledons usually broader than radicle.

The family Euphorbiaceae is here construed as having 317 genera associated into 49 tribes in 5 subfamilies. A reflection of the diversity of the family is that over 20 segregate families have been proposed (Webster, 1987). Hurusawa (1954) was the first modern author to propose a major dismantling of the family, with his recognition of Antidesmataceae, Euphorbiaceae (sensu stricto), Porantheraceae, and Ricinocarpaceae. This system, based on inflation of the subfamilies of Pax & Hoffmann (1931), has met with little acceptance.

More influential have been the efforts of Airy Shaw, who recognized seven segregate families: Androstachydaceae, Bischofiaceae, Hymenocardiaceae, Peraceae, Picrodendraceae, Stilaginaceae, and Uapacaceae (Airy Shaw, 1965, 1966). Among modern authors, the most extreme splitter is Meeuse (1990), who recognizes nine segregate families, plus the Pandaceae. Radcliffe-Smith in Carter & Radcliffe-Smith (1988) partially followed Airy Shaw in recognizing the Hymenocardiaceae and Pandaceae, but treats *Antidesma*, *Bischofia*, and *Uapaca* as anomalous genera of Euphorbiaceae. Of all these segregate taxa, only the family Pandaceae is recognized as distinct by Cronquist (1981) and Takhtajan (1980).

Key to the Subfamilies of Euphorbiaceae

1a. Locules of ovary each with 2 ovules (except in *Scagea*); milky latex, intraxylary phloem, and stinging hairs absent; indumentum simple or rarely lepidote or dendritic; embedded foliar glands rare; pollen grains binucleate.
- 2a. Leaves alternate (very rarely opposite), stipulate, blade simple and unlobed (trifoliolate in *Bischofia*); petals present or absent; pollen grains tricolporate to porate, sexine not with conspicuous spines (irregularly spiny in *Amanoa*); seeds ecarunculate ..... I. PHYLLANTHOIDEAE
- 2b. Leaves alternate, opposite, or whorled, stipulate or exstipulate, blade simple or trifoliolate; petals absent (except in *Croizatia*); pollen grains colpoidorate to porate, sexine spiny; seeds carunculate or ecarunculate, endosperm copious (except in *Hyaenanche* and *Picrodendron*) ..... II. OLDFIELDIOIDEAE

1b. Locules of ovary each with 1 ovule (except in *Dicoelia*); latex present or absent; indumentum various; pollen grains binucleate or trinucleate.
- 3a. Milky latex absent; laticifers (if present) inarticulate; leaves unlobed or lobed; indumentum simple or stellate; petals present or absent; pollen grains binucleate, mostly tricolporate or triporate ..... III. ACALYPHOIDEAE
- 3b. Latex milky or colored (rarely absent); laticifers articulate or inarticulate; leaves unlobed to compound; pollen grains binucleate or trinucleate.
  - 4a. Latex reddish or yellowish to milky (sometimes scanty or absent); laticifers articulate or inarticulate; leaves unlobed to lobed or compound; indumentum simple, stellate, dendritic, or lepidote; bracts usually not biglandular at base; sepals imbricate to valvate, usually completely covering anthers in bud; petals mostly present (at least in staminate flower); pollen grains tricolporate or more often porate or inaperturate, with "crotonoid" pattern of exinous processes ..... IV. CROTONOIDEAE
  - 4b. Latex whitish, often caustic or toxic; laticifers inarticulate; leaves usually unlobed; indumentum simple or absent, never stellate or lepidote (dendritic in *Mabea*); bracts often biglandular at base; sepals imbricate or reduced, anthers mostly not covered in bud; petals absent; pollen grains tricolporate, sexine mostly perforate-reticulate, never with "crotonoid" pattern ..... V. EUPHORBIOIDEAE

Subfamily I. PHYLLANTHOIDEAE

Ascherson, Fl. Prov. Brandenburg 1: 59. 1864. TYPE: *Phyllanthus* L.

Euphorbiaceae subordo Dispermae Zoll., Natuur-Geneesk. Arch. Ned.-Indië 2: 17. 1845.

Phyllanthaceae J. G. Agardh, Theor. Syst. Pl. 249. 1858 (as Phyllantheae); Klotzsch & Garcke, Monatsber. Königl. Preuss. Akad. Berlin 1859: 246. 1859.

Trees, shrubs, or herbs; indumentum simple (rarely branched; lepidote in *Hyeronima* and *Uapaca*); leaves alternate (very rarely opposite), spiral to distichous, usually stipulate; leaf blade simple, entire (except in *Drypetes* and *Bischofia*), without embedded foliar glands. Inflorescences axillary (rarely terminal), mostly racemiform or spiciform, or reduced to glomerules or solitary flowers; bracts eglandular, mostly inconspicuous. Sepals mostly 4–6, imbricate, sometimes connate; petals and disk present or absent; stamens (2–)4–8(–50), filaments free or united; pollen grains mostly 3–4-colporate (rarely porate; periporate in *Phyllanthus*), exine semitectate, rarely echinate; male ga-

metophyte binucleate; pistillode present or absent; carpels (1–)2–5(–20); styles mostly free except at base, usually bifid; ovules 2 in each locule, anatropous or hemitropous, nucellar beak sometimes prominent. Fruit capsular or less commonly baccate or drupaceous; seeds ecarunculate or with rudimentary caruncle; endosperm present or absent; cotyledons plane or folded. Base chromosome numbers mostly 12 or 13.

This large "basal" subfamily of Euphorbiaceae is so diverse that Meeuse (1990) proposed dividing it into six separate families. The 60 genera included are grouped into 10 tribes, a reduction from Webster (1975), where 13 tribes were recognized. The work of Levin (1986a, b, c) has shown that some proposed tribes need to be incorporated as subtribes within the Antidesmeae.

KEY TO THE TRIBES AND SUBTRIBES OF SUBFAMILY PHYLLANTHOIDEAE

1a. Leaves simple, mostly entire; styles usually bifid.
  2a. Flowers in axillary clusters (inflorescence axes less than 1 cm long except in some Phyllantheae); seeds with or without endosperm; leaves mostly with paracytic stomata, lacking tanniniferous epidermal cells.
    3a. Staminate disk extrastaminal or absent; leaves entire; ovary 2–3(–6)-locular; fruit mostly capsular or baccate, less commonly drupaceous.
      4a. Petals present, at least in staminate flowers; sepals imbricate; wood parenchyma conspicuous, fibers mostly thick-walled; vessel element perforations scalariform or simple; ovules anatropous; endosperm present or absent.
        5a. Pollen exine finely reticulate, not coarsely spinose; stipules deciduous ..... 1. WIELANDIEAE
        5b. Pollen exine coarsely and deeply reticulate or spinose; stipules persistent ..... 2. AMANOEAE
      4b. Petals absent, or if present then sepals valvate, or wood and ovule characters otherwise; endosperm usually present.
        6a. Sepals valvate; petals present, usually shorter than sepals ..... 3. BRIEDELIEAE
        6b. Sepals imbricate; petals absent, or if present then often as long as sepals . 4. PHYLLANTHEAE
    3b. Staminate disk intrastaminal; leaves often dentate; wood fibers thick-walled, not septate; fruit drupaceous; ovary 1–2-locular ..... 5. DRYPETEAE
  2b. Flowers in axillary or terminal spicate or racemose inflorescences (axis usually over 1 cm long; capitate in *Uapaca*); petals absent (or if present, inflorescence terminal); leaves with stomata paracytic or anomocytic; seeds with endosperm.
    7a. Fruits not winged; leaves with tanniniferous epidermal cells, not granulose-glandular; floral disk present or absent; pollen 3-colporate; styles usually bifid ..... 6. ANTIDESMEAE
    7b. Fruits winged, samaroid; leaves granulose-glandular, without tanniniferous epidermal cells; inflorescences amentlike; floral disk absent; pollen zonoporate; styles unlobed ..... 7. HYMENOCARDIEAE
1b. Leaves trifoliolate; inflorescence paniculate; flowers apetalous, floral disk absent; styles entire; fruits baccate ..... 8. BISCHOFIEAE

Tribe 1. WIELANDIEAE Baillon ex Hurusawa, J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 6: 339. 1954. Wielandiidées Baillon, Etude Gén. Euphorb. 568. 1858. Phyllantheae subtribe Wielandiinae Pax & Hoffm., Pflanzenr. 147. XV (Heft 81): 180. 1922. TYPE: *Wielandia* Baillon.

Monoecious or dioecious trees or shrubs; indumentum simple; leaves alternate, entire, pennineryed, eglandular; stipules deciduous. Inflorescences axillary; flowers in glomerules or the pistillate solitary; bracts inconspicuous. Sepals mostly 4–6, imbricate; petals usually 5; disk usually annular; stamens 5–10, free or filaments connate at base; anthers dehiscing longitudinally, connective not enlarged; pollen grains 3-colporate, semitectate, reticulate; pistillode present; carpels 3–5; styles bifid; ovules anatropous, usually with a single obturator. Fruit capsular; seeds 1 or 2 per locule; endosperm present or absent; embryo with cotyledons plane or folded, much longer than the radicle.

The taxa with the greatest numbers of unspecialized morphological features are gathered together in this tribe, which is unified on the basis of pollen morphology (Köhler, 1965) and leaf venation (Levin, 1986a, b, c). It is probably paraphyletic in cladistic terms, which is essentially inevitable for the basal tribe in a large family such as the Euphorbiaceae. Relationships among the nine genera appear reticulate, and it does not seem feasible to group them into subtribes. It is notable that all of the genera occur in South America, Africa, and the Indian Ocean islands, and only *Savia* extends into the Northern Hemisphere.

KEY TO THE GENERA OF TRIBE WIELANDIEAE

1a. Seeds with endosperm.
  2a. Stamens 8–10; sepals and petals mostly 4, very similar; ovary 4–5-locular ..... 1. *Heywoodia*

2b. Stamens mostly 5; sepals and petals mostly 5; ovary mostly 3-locular.
3a. Pistillate disk entire, not glandular ____ 2. *Savia*
3b. Pistillate disk glandular-lobed ____ 3. *Gonatogyne*
1b. Seeds with little or no endosperm.
4a. Staminate disk dissected ____ 4. *Petalodiscus*
4b. Staminate disk annular, sometimes lobed
5a. Ovary 3- or 4-locular.
6a. Monoecious.
7a. Leaves coriaceous; petals longer than sepals; stamens free except at base ____ 5. *Blotia*
7b. Leaves chartaceous; petals shorter than sepals; stamens connate into a column ____ 6. *Actephila*
6b. Dioecious; leaves coriaceous.
8a. Petals present; staminate flowers pedicellate.
9a. Styles dilated; staminate disk glabrous; stamens free from pistillode ____ 7. *Discocarpus*
9b. Styles slender; staminate disk pubescent; stamens adnate to pistillode ____ 8. *Lachnostylis*
8b. Petals absent; staminate flowers subsessile ____ 9. *Chonocentrum*
5b. Ovary 5-locular ____ 10. *Wielandia*

1. Heywoodia Sim, For. Fl. Cape Col. 326, pl. 140. 1907; Pax & Hoffm., Pflanzenr. 147. XV. (Heft 81): 280. 1922; Hutchinson, Kew Bull. 1922: 114. 1922; Milne-Redhead, Bull. Jard. Bot. Brux. 27: 327, pl. X. 1957; Radcliffe-Smith, Fl. Trop. E. Afr., Euphorb. 1: 85, fig. 12. 1987. TYPE: *Heywoodia lucens* Sim.

Monotypic; Uganda and Kenya south to Natal and Transkei. On the basis of foliar venation characters, Levin (1986b) suggested a relationship between *Heywoodia* and *Astrocasia*, and regarded both genera as closer to the tribe Phyllantheae. There are indeed some resemblances between *Heywoodia* and *Astrocasia*, but the former genus seems the more primitive, and appears to me as perhaps nearest in morphological characters to the hypothetical ancestor of the family. This would not preclude an affinity with *Astrocasia*, which may connect the tribes Wielandieae and Phyllantheae.

2. Savia Willdenow, Sp. Pl. 4: 771. 1805; Muell. Arg. in DC. Prodr. 15(2): 228. 1866; Bentham, Gen. Pl. 3: 270. 1880; Fawc. & Rend., Fl. Jam. 4: 271. 1920; Pax & Hoffm., Pflanzenr. 147. XV (Heft 81): 181. 1922; Urban, Repert. Sp. Nov. 28: 209. 1928; Alain, Fl. Cuba 3: 41. 1953; Webster, J. Arnold Arbor. 48: 325. 1967; Taxon 31: 535. 1982; Radcliffe-Smith, Kew Bull. 27: 508. 1972; Fl. Trop. E. Afr., Euphorb. 1: 83, fig. 11. 1987. TYPE: *Savia sessiliflora* (Sw.) Willd.

Kleinodendron Smith & Downs, Sellowia 16: 177. 1964. TYPE: *Kleinodendron riosulense* Smith & Downs [= *Savia dictyocarpa* Muell. Arg.].

About 25 species of America, Africa, and Madagascar. Three sections have been recognized: sect. *Savia*, 2 spp., the type and *S. dictyocarpa* of Brazil; sect. *Heterosavia* Urb., ca. 20 spp. of the West Indies and Madagascar; and the recently described sect. *Afrosavia* Radcl.-Sm. of Kenya (which as noted below actually belongs to *Petalodiscus*). A number of other genera of tribe Wielandieae have been included in *Savia* by Mueller and other workers.

3. Gonatogyne Muell. Arg., Fl. Bras. 11(2): 13. 1873; Pax & Hoffm., Repert. Sp. Nov. 31: 190. 1933. *Savia* sect. *Gonatogyne* ("Klotzsch") Pax & Hoffm., Pflanzenr. 147. XV (Heft 81): 187. 1922. TYPE: *Gonatogyne brasiliensis* (Baillon) Muell. Arg. [*Amanoa ? brasiliensis* Baillon].

Monotypic; Brazil.

4. Petalodiscus (Baillon) Pax, Natürl. Pflanzenfam. I. 3(5): 15. 1890. *Savia* sect. *Petalodiscus* Baillon, Etude Gén. Euphorb. 571. 1858. TYPE: *Petalodiscus platyrhachis* (Baillon) Pax (lectotype, selected here; this was the species illustrated by Pax, loc. cit.).

A genus of five or six species endemic to Madagascar; combined with *Savia* by Pax & Hoffmann (1922, 1931) and Leandri (1958), but differing from *Savia* in being monoecious and having exalbuminous seeds.

5. Blotia Leandri, Mém. Inst. Sci. Madag. 88: 240. 1957; Fl. Madag. 111: 126. 1958. *Savia* sect. *Charidia* Baillon, Etude Gén. Euphorb. 572. 1858; Muell. Arg., DC. Prodr. 15(2): 229. 1866. *Petalodiscus* sect. *Charidia* (Baillon) Pax, Natürl. Pflanzenfam. I. 3(5): 15. 1890. TYPE: *Blotia oblongifolia* (Baillon) Leandri [*Savia oblongifolia* Baill.].

This genus of five or six Madagascan species is closely related to *Petalodiscus* and may not be distinct.

6. Actephila Blume, Bijdr. Fl. Ned. Ind. 581. 1825; Muell. Arg., DC. Prodr. 15(2): 221. 1866; Baillon, Adansonia I. 6: 231. 1866; Bentham, Gen. Pl. 3: 269. 1880; J. J. Smith, Add. Cogn. Fl. Arb. Jav. 12: 45. 1910; Pax & Hoffm., Pflanzenr. 147. XV (Heft 81): 191. 1922; Airy Shaw, Kew Bull. 25: 496. 1971; Kew Bull. Add. Ser. 8: 21. 1980. TYPE: *Actephila javanica* Miq.

Anomospermum Dalzell, Hook. J. Bot. Kew Gard. Misc. 3: 228. 1851 (non Miers, 1851). TYPE: *Anomospermum excelsum* Dalz. [= *Actephila excelsa* (Dalz.) Muell. Arg.].

An Asian/Australasian genus of ca. 20 described species, still poorly understood taxonomically. The position of the genus has been variously interpreted. Pax & Hoffmann (1922) associated it with *Amanoa*, which has similar flowers but very different pollen. Köhler (1965) pointed out a palynological similarity to *Andrachne*, and Levin (1986 a, b, c) found a resemblance in leaf venation to that genus. However, the exalbuminous seeds with plicate embryo of *Actephila* would appear to rule out a close association with *Andrachne*. It is worth noting that Mennega (1987) recommended assignment of *Actephila* to the Wielandieae. For the present, it seems best to retain *Actephila* in the tribe Wielandieae.

7. Discocarpus Klotzsch, Arch. Naturgesch. 7: 201. 1841; Muell. Arg., DC. Prodr. 15(2): 223. 1866; Fl. Bras. 11(1): 11, t. 2. 1873; Benth., Gen. Pl. 3: 269. 1880; Pax & Hoffm., Pflanzenr. 147. XV (Heft 81): 202. 1922; Jablonski, Mem. New York Bot. Gard. 17(1): 84. 1967. TYPE: *Discocarpus essequiboensis* Klotzsch.

According to the recent treatment of Jablonski, the five species of *Discocarpus* are restricted to the Amazonian/Guianan region of South America. The phylogenetic position of *Discocarpus* is somewhat uncertain. Pax & Hoffmann (1922) assigned it to a separate subtribe (including *Lachnostylis*); Köhler (1965) suggested it was close to Amanoeae and Bridelieae; and Mennega (1987) regarded it as out of place in the Wielandieae.

8. Lachnostylis Turczaninov, Bull. Soc. Imp. Naturalistes Moscou 19: 503. 1846; Muell. Arg., DC. Prodr. 15(2): 224. 1866; Bentham, Hook. Ic. Pl. 13: 61, t. 1279. 1879; Gen. Pl. 3: Dyer, Gen. S. Afr. Fl. Pl. 1: 309. 1975. TYPE: *Lachnostylis capensis* Turcz. [= *Lachnostylis hirta* (L.) Muell. Arg.].

This genus, endemic to South Africa, includes a single variable species or, according to some workers (e.g., Dyer), two species. Although combined with *Discocarpus* by Pax & Hoffmann (1922), it differs in a number of characters.

9. Chonocentrum Pierre ex Pax & Hoffmann, Pflanzenr. 147. XV (Heft 81): 205. 1922; Jablonski, Mem. New York Bot. Gard. 17: 121. 1967. TYPE: *Chonocentrum cyathophorum* (Muell. Arg.) Pax & Hoffm. [*Drypetes cyathophora* Muell. Arg.].

A monotypic genus of Amazonian South America, regarded by Pax & Hoffmann as related to *Discocarpus*; however, the pollen is still unstudied, and its relationships must be regarded as uncertain.

10. Wielandia Baillon, Etude Gén. Euphorb. 568. 1858; Bentham, Gen. Pl. 3: 270. 1880; Hemsley, Hook. Ic. Pl. 29: t. 2813. 1906; Pax & Hoffm., Pflanzenr. 147. XV (Heft 81): 181. 1922; Leandri, Notul. Syst. (Paris) 7: 190. 1939; Fl. Madag. 111(1): 135. 1958. TYPE: *Wielandia elegans* Baillon.

Monotypic; restricted to Madagascar and the Seychelles. Although combined with *Savia* by Mueller, *Wielandia* appears closer to *Petalodiscus* by virtue of its exalbuminous seeds and monoecious flower production.

Tribe 2. AMANOEAE (Pax & Hoffmann) Webster, Taxon 24: 594. 1975. Phyllantheae subtribe Amanoinae Pax & Hoffm., Pflanzenr. 147. XV (Heft 81): 190. 1922. TYPE: *Amanoa* Aublet.

Monoecious trees; indumentum simple (extremely scarce to absent); leaves alternate, simple, entire, penninerved, eglandular; stipules persistent, sometimes adnate to petiole. Flowers in glomerules, these sometimes forming spikes; bracts conspicuous or inconspicuous. Sepals and petals 5, imbricate; staminate disk annular or dissected; stamens 5, free; anthers introrse; pollen grains tricolporate, very coarsely reticulate or irregularly spinose; pistillode prominent; pistillate disk cupular; ovary 3-locular; ovules anatropous; styles twice bifid or dilated, emarginate; fruit a tardily dehiscent capsule; seeds 1 per locule; endosperm present, scanty or absent; cotyledons massive but not plicate, much longer than radicle.

As here interpreted, the tribe Amanoeae includes the genera *Amanoa* and *Pentabrachion*. In the original circumscription of the tribe (Webster,

1975), *Actephila* was also included. However, evidence from pollen morphology (Köhler, 1965), leaf venation (Levin, 1986a, b, c), and wood anatomy (Mennega, 1987) argues against a close association of *Amanoa* and *Actephila*.

KEY TO THE GENERA OF TRIBE AMANOEAE

1a. Stipules not intrapetiolar; floral bracts inconspicuous, not indurate; styles slender, twice bifid; fruit thin-walled, seeds 2 per locule, endosperm present ..... 11. *Pentabrachion*

1b. Stipules ± intrapetiolar; floral bracts conspicuous, indurate; styles dilated, emarginate; fruit thick-walled, seeds 1 per locule; endosperm absent ..... 12. *Amanoa*

11. Pentabrachion Muell. Arg., Flora 47: 532. 1864; DC. Prodr. 15(2): 223. 1866 (as *Pentabrachium*); Pax & Hoffm., Pflanzenr. 147. XV (Heft 81): 188. 1922. TYPE: *Pentabrachion reticulatum* Muell. Arg.

Monotypic; West Africa (Cameroon, Gabon). Levin (1986a, b, c) suggested a possible relationship to *Dicoelia* on the basis of foliar venation characters, but this is not supported by pollen characters (Köhler, 1965). Indeed, Köhler associated *Pentabrachion* with the Amanoeae and Bridelieae because of its coarsely reticulate pollen grains. It appears that this palynological similarity may be a better guide to affinity, so *Pentabrachion* is here placed in the same tribe with *Amanoa*, despite the obvious differences between the genera.

12. Amanoa Aublet, Fl. Guiane Fr. 256, pl. 101. 1775; Muell. Arg., DC. Prodr. 15(2): 219. 1866; Bentham, Gen. Pl. 3: 268. 1880; Baillon, in Grandidier, Atlas Hist. Madag. Pl. tt. 210, 211. 1892; Pax & Hoffm., Pflanzenr. 147. XV (Heft 81): 195. 1922; Jablonski, Mem. New York Bot. Gard. 17: 82. 1967; Webster, Ann. Missouri Bot. 54: 1968; Hayden, Brittonia 4: 260. 1990. TYPE: *Amanoa guianensis* Aublet.

A mainly neotropical genus of 16 species; the three African species have been referred to an endemic section.

Tribe 3. BRIEDELIEAE Muell. Arg., Bot. Zeit. 22: 324. 1864 (as Bridelieae). Tribe Biovulatae sect. Bridelieae Thwaites, Enum. Pl. Zeyl. 279. 1861. Antidesmataceae subfam. Bridelioideae Hurusawa, J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 6: 321. 1954. TYPE: *Briedelia* Willd.

Monoecious (rarely dioecious) trees or shrubs; leaves alternate, entire, pinnately veined, without laminar glands; stipules usually deciduous. Flowers in bracteate glomerules, these axillary or in spikes. Sepals mostly 5, valvate; petals 5, imbricate or valvate, usually smaller than the sepals, sometimes dentate or reduced; disk annular or dissected; stamens mostly 5, filaments connate into a column; anthers introrse; pollen grains tricolporate, reticulate or striate; pistillode present; pistillate sepals 5, imbricate or valvate, deciduous; disk annular or cupular; ovary 2- or 3-(rarely 4-)locular; ovules anatropous; styles 2- or 4-fid; fruit capsular or drupaceous, 1–3-celled; seeds with endosperm; cotyledons much longer and broader than the radicle.

The tribe has traditionally been considered to comprise two closely related genera, *Cleistanthus* and *Briedelia*. However, the diagnostic characters are not entirely satisfactory (as indicated, for example, in the complicated distinctions in the key of Léonard, 1962a) and generic delimitation requires further study. Baillon (1858) regarded *Briedelia* as being close to *Amanoa*, and Köhler (1965) saw resemblances between pollen of *Amanoa* and the African species of *Cleistanthus*; following the latter's suggestion, it would be possible to associate the Amanoeae and Bridelieae as subtribes of a single tribe. Nevertheless, neither the floral nor pollen characters of the Bridelieae appear sufficiently close to *Amanoa* to associate them in the same tribe.

KEY TO THE GENERA OF TRIBE BRIEDELIEAE

1a. Ovary mainly of 3 carpels (rarely 2 or 4); fruits capsular, lobed, mainly 3-locular with 2 seeds per locule; leaf ventation mainly reticulate ..... 13. *Cleistanthus*

1b. Ovary mainly of 2 carpels (rarely 3); fruits drupaceous or rarely capsular, unlobed, 1- or 2-locular with 1 seed per locule; leaf venation mainly percurrent ..... 14. *Briedelia*

13. Cleistanthus Hooker f. ex Planchon, Hook. Ic. Pl. 8: t. 779. 1848; Muell. Arg., DC. Prodr. 15(2): 503. 1866; Bentham, Gen. Pl. 3(1): 268. 1880; Jablonski, Pflanzenr. 147. VIII (Heft 65): 8. 1915; Gagnepain, Fl. Indochine 5: 482. 1926; Croizat, J. Arnold Arbor. 23: 38. 1942; Leandri, Fl. Madag. 111: 181. 1958; Léonard, Bull. Jard. Bot. Brux. 30: 421. 1960; Fl. Congo 8(1): 5. 1962; Radcliffe-Smith, Fl. Trop. E. Afr., Euphorb. 130. 1987. TYPE: *Cleistanthus polystachyus* Hook. f.

Nanopetalum Hassk., Versl. Meded. Afd. Natuurk. Kon.

Akad. Wetensch. Amsterdam 4: 140. 1856. TYPE: *Nanopetalum myrianthum* Hassk. [= *Cleistanthus myrianthus* (Hassk.) Kurz].

Leiopyxis Miquel, Fl. Ned. Ind., Erste Bijv. 445. 1861. TYPE: *Leiopyxis sumatrana* Miq. [= *Cleistanthus sumatranus* (Miq.) Muell. Arg.].

Lebidieropsis Muell. Arg., Linnaea 32: 80. 1863. TYPE: *Lebidieropsis collina* (Roxb.) Muell. Arg. [= *Cleistanthus collinus* (Roxb.) Benth.].

Schistostigma Lauterbach, Fl. Deutsches Schutzgeb. Nachtr. 299. 1905. TYPE: *Schistostigma papuanum* Laut. [= *Cleistanthus papuanus* (Laut.) Jabl.].

Paracleistus Gagnepain, Bull. Soc. Bot. France 70: 499. 1923. TYPE: *Paracleistus subgracilis* Gagnep. [= *Cleistanthus saichikii* Merr. & Chun; lectotype, designated by Wheeler, 1975.].

Godefroya Gagnepain, Bull. Soc. Bot. France 70: 435. 1923. TYPE: *Godefroya rotundata* (Jabl.) Gagnep. [= *Cleistanthus rotundatus* Jabl.].

A large and rather diverse genus of over 100 species, of which about 30 occur in Africa/Madagascar and the rest in tropical Asia, from India to northern Australia and Melanesia. Both Köhler (1965) and Levin (1986a) found *Cleistanthus* to be heterogeneous on the basis of pollen and leaf characters, respectively; clearly, generic limits in the tribe need to be critically reevaluated.

14. Briedelia Willdenow, Sp. Pl. 4(2): 978. 1805; Sprengel, Anleit. Kenntn. Gew. 2(2): 887. 1818 (as *Bridelia*); Muell. Arg., DC. Prodr. 15(2): 493. 1866; Pfeiffer, Nomencl. Bot. 1(1): 467. 1874; Bentham, Gen. Pl. 3(1): 267. 1880; Gehrmann, Bot. Jahrb. 41(Beibl. 95): 1. 1908; Hutchinson, Fl. Trop. Afr. 6(1): 611. 1912; Jablonski, Pflanzenr. 147. VIII (Heft 65): 54. 1915; Leandri, Fl. Madag. 111: 192. 1958; Léonard, Fl. Congo 8(1): 27. 1962; Radcliffe-Smith, Fl. E. Trop. Afr., Euphorb. 120. 1987; Chapman, Austral. Pl. Name Index 476. 1991. TYPE: *Briedelia scandens* (Roxb.) Willd. [*Clutyia scandens* Roxb.; lectotype, selected here; of the 3 species included in the original description of Willdenow, it is the only one placed in subg. *Briedelia* by Gehrmann (1908) and of which Willdenow saw herbarium material].

Candelabria Hochstetter, Flora 26: 79. 1843. TYPE: *Candelabria micrantha* Hochst. [= *Briedelia micrantha* (Hochst.) Baillon].

Neogoetzea Pax, Bot. Jahrb. 28: 419. 1900. TYPE: *Neogoetzea brideliifolia* Pax [= *Briedelia brideliifolia* (Pax) Fedde].

Gentilia Beille, Compte Rend. Acad. Sci. Paris 114: 1294. 1907. TYPE: *Gentilia hygrophila* Beille [= *Briedelia ndellensis* Beille].

Tzellemtinia Chiovenda, Ann. Bot. Roma 9: 55. 1911. TYPE: *Tzellemtinia nervosa* Chiov. [= *Briedelia scleroneura* Muell. Arg.].

An Old World genus of more than 60 species, the majority Asian. I agree with Pfeiffer (1874) and Chapman (1991) in adopting Willdenow's original spelling for the genus; Sprengel's correction to match the name of the botanist honored (S. E. Bridel) is contrary to the current rules of nomenclature.

Tribe 4. PHYLLANTHEAE Dumortier, Anal. Fam. Pl. 45. 1829. Euphorbiaceae sect. Phyllantheae Blume, Bijdr. 578. 1826 (nom. illeg.). Ordnung Phyllanthaceae Kl. & Gcke., Monatsber. Königl. Akad. Wiss. Berlin 1859: 246. 1859. TYPE: *Phyllanthus* L.

Monoecious or dioecious trees, shrubs, or herbs; leaves alternate, entire, pinnately veined, without laminar glands; stipules persistent or deciduous. Flowers in axillary racemes or glomerules, bracts inconspicuous. Staminate sepals 4–6, free or connate, imbricate; petals present or absent; disk extrastaminal, dissected or entire (rarely absent); stamens (2–)3–5(–10), filaments free or connate; anthers mostly extrorse; pollen grains prolate to oblate, mostly 3-colporate (sometimes stephanocolporate or porate); pistillode present or absent; pistillate sepals mostly 5, imbricate, persistent or deciduous; disk cupular to lobed (less commonly dissected or absent); ovary mostly 3–5-locular; ovules anatropous or hemitropous; styles bifid or entire (rarely multifid). Fruit usually capsular (rarely baccate or drupaceous); seeds 1 or 2 per locule; endosperm present; embryo with cotyledons broader than and at least equal in length with the radicle.

As here interpreted, tribe Phyllantheae is considerably narrower in scope than the circumscription of Pax & Hoffmann (1922), but broader than that of Webster (1975). The relationships of some of the taxa (e.g., *Astrocasia, Leptopus*) point toward the Wielandieae, but Phyllantheae are anatomically more advanced in such characters as septate fibers and scarcity of scalariform perforations. The inclusion of petaliferous and apetalous genera together seems justified by similarities in pollen (Punt, 1962; Köhler, 1965) and some of the leaf venation characters pointed out by Levin (1986a).

Subdivision of this heterogeneous tribe into subtribes is still controversial; the present classification with six subtribes must be considered provisional. The distinction between anatropous and hemitropous ovules, pointed out by Baillon (1858), appears systematically significant even though not all genera have yet been carefully studied, and there may prove to be transitional stages.

KEY TO THE SUBTRIBES OF TRIBE PHYLLANTHEAE

1a. Petals present; ovules anatropous; seeds smooth.
  2a. Pistillate sepals deciduous; staminal column adnate to peltate pistillode ..... 4a. Astrocasiinae
  2b. Pistillate sepals persistent; stamens free or connate below ..... 4b. Leptopinae
1b. Petals absent (except in some Andrachninae); ovules anatropous or hemitropous; seeds smooth or sculptured.
  3a. Ovules anatropous; pistillode present.
    4a. Staminate disk annular; pollen grains reticulate; seed coat dull or sculptured ..... 4c. Pseudolachnostylidinae
    4b. Staminate disk dissected; pollen grains verruculose; seed coat blackish, smooth ..... 4d. Securineginae
  3b. Ovules hemitropous; staminate disk annular or dissected; pistillode present or absent.
    5a. Petals present; stamens 5, free; staminate disk dissected .... 4e. Andrachninae
    5b. Petals absent; stamens 2–10 or more, free or connate; staminate disk annular or dissected ..... 4f. Flueggeinae

Subtribe 4a. ASTROCASIINAE Webster, Syst. Bot. 17: 315. 1992. TYPE: *Astrocasia* Rob. & Greenm.

Dioecious (or subdioecious) trees or shrubs; stipules deciduous; flowers in axillary glomerules; staminate sepals 5; disk annular; stamens 5, filaments connate into a column; pollen grains 3-colporate, reticulate; pistillode peltate; pistillate sepals 5, deciduous; disk annular; ovary 3-locular; ovules anatropous; styles bifid; fruits capsular; seeds 1 or 2 per locule, smooth; cotyledons much longer than radicle.

This monogeneric tribe includes only the type genus *Astrocasia*, which was included in tribe Wielandieae by Webster (1975), following Pax & Hoffmann (1922). However, Pax & Hoffmann referred *Astrocasia* to the Wielandieae on the basis of a mistaken interpretation of the floral morphology. Pollen studies of Köhler (1965) and leaf venation studies of Levin (1986a, b, c) suggest, on the contrary, that *Astrocasia* shows more similarities to the tribe Phyllantheae, particularly to genera of subtribes Leptopinae and Pseudolachnostylidinae.

15. Astrocasia Robinson & Greenman, Bot. Jahrb. 36 (Beibl. 80): 19. 1905; Pax & Hoffm., Pflanzenr. 147. XV (Heft 81): 189. 1922; Webster, Syst. Bot. 17: 311. 1992. TYPE: *Astrocasia phyllanthoides* Rob. & Greenm. [= *Astrocasia tremula* (Griseb.) Webster].

A neotropical genus of five species distributed from Mexico and Cuba south to Bolivia and eastern Brazil.

Subtribe 4b. LEPTOPINAE Webster, subtribe nov. TYPE: *Leptopus* Dcne.

Stipulae persistentae; petala conspicua; stamina 5, filamenta libera vel connata; pistillodio trifidum; sepala pistillata persistentia; ovarium 3-loculare, ovulis anatropis; fructus capsularis; semina laevia.

Dioecious shrubs or herbs; stipules persistent; flowers in axillary glomerules; staminate sepals 5; disk annular or dissected; stamens 5, filaments free or connate below; pollen grains 3-colporate, reticulate; pistillode 3-fid; pistillate sepals 5, persistent; disk annular or dissected; ovary 3-locular; ovules anatropous; styles bifid; fruit capsular; seeds 2 per locule, testa smooth; cotyledons much longer than radicle.

This subtribe includes only the single genus *Leptopus*, which was submerged in *Andrachne* by Mueller (1866), Bentham (1880), and Pax & Hoffmann (1922). However, *Leptopus* differs from *Andrachne* (sensu stricto) in its anatropous ovules, and appears to represent a connecting link between *Astrocasia* and *Andrachne*. It therefore appears best to assign it to a separate subtribe.

16. Leptopus Decaisne, in Jacquemont, Voy. Inde Bot. 4: 155. 1836; Pojarkova, Not. Syst. Herb. Inst. Bot. Acad. Sci. USSR 20: 269. 1960; Li Ping-T'ao, Notes Roy. Bot. Gard. Edinburgh 40: 467. 1983. TYPE: *Leptopus cordifolius* Dcne.

Lepidanthus Nuttall, Trans. Amer. Phil. Soc. 5: 175. 1837 (non *Lepidanthus* Nees, 1830). TYPE: *Lepidanthus phyllanthoides* Nutt. (loc. cit.) [= **Leptopus phyllanthoides** (Nutt.) Webster, comb. nov.].

Thelypetalum Gagnepain, Bull. Soc. Bot. France 71: 876. 1924. TYPE: *Thelypetalum pierrei* Gagnep. [= *Leptopus australis* (Zoll.) Pojark.].

Chorisandrachne Airy Shaw, Kew Bull. 23: 40. 1969. TYPE: *Chorisandrachne diplosperma* Airy Shaw [= **Leptopus diplospermus** (Airy Shaw) Webster, comb. nov.].

A genus of ca. 10 species of widely scattered distribution in the Old World (India to China, Indonesia, and tropical Australia) and North America (Mexico, southern U.S., and Greater Antilles).

Subtribe 4c. PSEUDOLACHNOSTYLIDINAE Pax & Hoffmann, Pflanzenr. 147. XV (Heft 81): 206. 1922. TYPE: *Pseudolachnostylis* Pax.

Monoecious or dioecious trees, shrubs, or undershrubs; stipules persistent or deciduous; flowers in axillary glomerules or cymes, bracts inconspicuous; staminate sepals 5, petals absent; disk annular; stamens usually 5, filaments free or connate; pollen grains 3-colporate, reticulate; pistillode present; pistillate sepals 5, persistent or deciduous; petals absent; disk annular; ovary 3-locular; ovules anatropous; styles bifid; fruit capsular; seeds 1 or 2 per locule, testa smooth or sculptured; cotyledons much longer than radicle.

This subtribe of six genera is heterogeneous and possibly unnatural, as it is quite possible that *Pseudolachnostylis* and *Keayodendron* may not be closely related to the other genera.

KEY TO THE GENERA OF SUBTRIBE PSEUDOLACHNOSTYLIDINAE

1a. Fruit capsular, 3-locular, with 3–6 seeds; staminate disk annular.
  2a. Capsule thin-walled; cymes (glomerules) not pedunculate; seeds with sculptured testa; pistillate sepals persistent.
    3a. Chalaza dorsal on seed; staminate flowers subsessile ____ 17. *Chascotheca*
    3b. Chalaza ventral; staminate flowers pedicellate.
      4a. Filaments free from pistillode.
        5a. Stipules foliaceous, persistent; sepals broad and imbricate ____ 18. *Zimmermannia*
        5b. Stipules narrow, deciduous; sepals linear-lanceolate, not imbricate ____ 19. *Zimmermanniopsis*
      4b. Filaments connate to pistillode; stipules narrow ____ 20. *Meineckia*
  2b. Capsule thick-walled; pistillate cymes pedunculate; seeds with smooth testa; pistillate sepals deciduous; filaments connate ____ 21. *Pseudolachnostylis*
1b. Fruit drupaceous, 2-locular, with one seed; staminate disk dissected ____ 22. *Keayodendron*

17. Chascotheca Urban, Symb. Ant. 5: 14. 1904; Alain, Fl. Cuba 3: 44. 1953. *Chaenotheca* Urban, Symb. Ant. 3: 284. 1902 (non T. M. Fries, 1860). TYPE: *Chascotheca neopeltandra* (Griseb.) Urb.

Three species have been described in this Greater Antillean genus (Cuba and Hispaniola), but *Chascotheca domingensis* (Urb.) Urb. is probably a synonym of the type species.

18. Zimmermannia Pax, Bot. Jahrb. 45: 235. 1910; Hutchinson, Fl. Trop. Afr. 6(1): 739. 1912; Verdcourt, Kew Bull. 9: 38. 1954; Poole, Kew Bull. 36: 129. 1981; Radcliffe-Smith, Fl. E. Trop. Afr. Euphorb. 71. 1987. TYPE: *Zimmermannia capillipes* Pax.

As interpreted by Radcliffe-Smith (1987), *Zimmermannia* includes six east African species, plus a dubious Madagascan species transitional to *Meineckia*.

19. Zimmermanniopsis Radcliffe-Smith, Kew Bull. 45: 152. 1990. TYPE: *Zimmermanniopsis uzungwaensis* Radcl.-Sm.

A monotypic genus from Tanzania (Iringa Distr.), very close to *Zimmermannia*, and questionably distinct.

20. Meineckia Baillon, Etude Gén. Euphorb. 586. 1858; Webster, Acta Bot. Neerl. 14: 323. 1965; Radcliffe-Smith, Hook. Ic. Pl. 37: t. 3698. 1971; Brunel & Roux, Bull. Mus. Hist. Nat. Paris, IV. 4: 79. 1982; Radcliffe-Smith, Fl. Trop. E. Afr. Euphorb. 76. 1987. TYPE: *Meineckia phyllanthoides* Baillon.

Cluytiandra Muell. Arg., J. Bot. 2: 328. 1864. TYPE: *Cluytiandra trichopoda* Muell. Arg. [= *Meineckia trichopoda* (Muell. Arg.) Webster].

Peltandra Wight, Icon. Pl. Ind. Or. 5(2): 24. 1852 (non *Peltandra* Raf., 1819). *Neopeltandra* Gamble, Fl. Madras 1285. 1925. TYPE: *Peltandra parvifolia* Wight [= *Meineckia parvifolia* (Wight) Webster; lectotype].

A genus of 20 species with a disjunct distribution in the New World and Old World, from Mexico to Colombia and Brazil, and from central Africa to Madagascar, southern India, Sri Lanka, and Assam.

21. Pseudolachnostylis Pax, Bot. Jahrb. 23: 19. 1899; Hutchinson, Hook. Ic. Pl. 31: t. 3011. 1915; Pax & Hoffm., Pflanzenr. 147. XV (Heft 81): 206. 1922; Phillips, Gen. S. Afr. Pl. ed. 2, 457. 1951; Radcliffe-Smith, Fl. E. Trop. Afr. Euphorb. 80. 1987. TYPE: *Pseudolachnostylis dekindtii* Pax.

An African genus of six described species, reduced by Radcliffe-Smith (1987) to four varieties of *P. maprouneifolia* Pax. The phylogenetic position of *Pseudolachnostylis* remains uncertain, although the disposition of Pax & Hoffmann (1922) in locating it adjacent to *Meineckia* is followed here. However, the pedunculate inflorescence and

massive fruits of *Pseudolachnostylis* are quite different from the preceding genera, and it is not clear that it really belongs in the same subtribe. Köhler (1965) has proposed that *Pseudolachnostylis* be classified with *Amanoa* because of its coarsely reticulate pollen grains and large fruits. However, the flowers differ from those of *Amanoa* in lacking petals or conspicuous bracts, and in having bifid styles; furthermore, the plants are dioecious, and the stipules are deciduous. Because of all these differences, it seems possible that the similarity in pollen ornamentation represents convergence rather than close affinity.

22. Keayodendron Leandri, Soc. Bot. France 105: 517. 1959. TYPE: *Keayodendron bridelioides* (Mildbr. ex Hutch. & Dalz.) Leandri.

A monotypic genus from tropical west Africa, still poorly known. As the specific epithet suggests, the fruits and aspect suggest *Briedelia*, but the flowers are apetalous, with imbricate sepals. *Keayodendron* is diffidently referred to this subtribe for lack of a better alternative.

Subtribe 4d. SECURINEGINAE Muell. Arg., DC. Prodr. 15(2): 446. 1866. TYPE: *Securinega* Comm. ex Juss.

Dioecious shrubs or small trees; stipules deciduous; flowers in axillary glomerules, bracts inconspicuous; staminate sepals 5; petals absent; disk dissected; stamens 5(–10), free; pollen grains 3-colporate, sexine verruculose; pistillode present; pistillate sepals 5, persistent; disk angled or absent; ovary 3-locular; ovules anatropous; styles bifid; fruit capsular; seeds 1 or 2 per locule, testa dark and smooth; cotyledons about equaling the radicle.

Although Mueller's name is applied to this subtribe, its present circumscription is very different, since Mueller (1866) included *Hymenocardia* and genera of subtribe Scepinae. The distinctive pollen and seeds of *Securinega* set it apart from other taxa in tribe Phyllantheae and suggest a possible affinity with subfamily Oldfieldioideae.

23. Securinega Commerson ex Jussieu, Gen. Pl. 388. 1789 (nom. cons.); Leandri, Fl. Madag. 111: 107. 1958. TYPE: *Securinega durissima* J. F. Gmel. (typ. cons.).

A Malagasian genus of five closely related species, the type from Reunion and Mauritius, the others from Madagascar. The majority of workers have confounded the genus with *Flueggea*, and only Leandri among modern writers has presented the genus as accepted here.

Subtribe 4e. ANDRACHNINAE Muell. Arg., Linnaea 34: 64. 1865 (as Andrachneae); Pax, Nat. Pflanzenfam. ed. 1, 3(5): 15. 1890; Pax & Hoffm., Pflanzenr. 147. XV (Heft 81): 169. 1922. TYPE: *Andrachne* L.

Monoecious herbs or subshrubs; stipules persistent; flowers in axillary glomerules, bracts inconspicuous; staminate sepals and petals 5; disk dissected; stamens 5, filaments free or connate; pollen grains 3-colporate, sexine reticulate or striate; pistillode present; pistillate sepals 5, persistent; petals 5; disk annular or dissected; ovary 3-locular; ovules hemitropous; styles bifid; fruit capsular; seeds 2 per locule, testa sculptured; cotyledons much longer than radicle.

The subtribe includes only the genus *Andrachne* (sensu stricto); Mueller (1866) and most later workers included *Leptopus* within *Andrachne*. Except for the presence of petals, species of *Andrachne* resemble herbaceous species of *Phyllanthus*; however, it is not clear whether this indicates close affinity. Earlier (Webster, 1975), I associated the Australian genus *Poranthera* with *Andrachne* because of similarity in the pollen pointed out by Köhler (1965). However, other characters of *Poranthera* now seem to me to point toward affinity with tribe Antidesmeae.

24. Andrachne L., Spec. Pl. 1014. 1753; Gen. Pl. ed. 5, 444. 1754; Muell. Arg., DC. Prodr. 15(2): 232. 1866; Bentham, Gen. Pl. 3: 270. 1880; Kossinki, Bot. Mater. Gerb. Glavn. Bot. Sada RSFSR 2: 77. 1921; Pax & Hoffm., Pflanzenr. 147. XV (Heft 81): 169. 1922; Croizat, J. Wash. Acad. Sci. 33: 11. 1942; Vindt, Trav. Inst. Sci. Chérifien 6: 4. 1953; Pojarkova, Not. Syst. Herb. Inst. Bot. Acad. Sci. USSR 20: 256. 1960; Webster, J. Arnold Arbor. 48: 327. 1967; Radcliffe-Smith, Fl. Trop. E. Afr., Euphorb. 7. 1987; Gilbert & Thulin, Nordic J. Bot. 8: 159. 1988. TYPE: *Andrachne telephioides* L. [lectotype, designated by Small in Britton & Brown, Ill. Fl. N. U.S. ed. 2, 2: 453. 1913].

Eraclissa Forsskål, Fl. Aegypt.-Arab. 208. 1775. TYPE: *Eraclissa hexagyna* Forssk. [= *Andrachne telephioides* L.].

Telephioides Gomez Ortega, Tabulae Bot. 15. 1773. TYPE: *Telephioides procumbens* Moench [= *Andrachne telephioides* L.].

Phyllanthidea Didrichsen, Vidensk. Medd. Naturh. Foren. Kjøbenhavn 1857: 450. 1857. TYPE: *Phyllanthidea microphylla* (Lam.) Didr. [= *Andrachne microphylla* (Lam.) Baillon].

In the restricted circumscription adopted here, *Andrachne* includes about 15 species with a primarily Tethyan distribution from Persia through the Mediterranean to the West Indies, with one species (*A. microphylla*) disjunct from Baja California to Pacific South America. The majority of species listed under *Andrachne* by most authors are better classified in a separate genus *Leptopus*.

Subtribe 4f. FLUEGGEINAE Muell. Arg., Linnaea 34: 64. 1865 (as Flüggeae). TYPE: *Flueggea* Willd.

Tribe Phyllantheae subtribe Euphyllantheae Muell. Arg., Linnaea 34: 64. 1865 (nom. illeg.). TYPE: *Phyllanthus* L.

Tribe Phyllantheae subtribe Sauropodeae Muell. Arg., Linnaea 34: 64. 1865. TYPE: *Sauropus* Bl.

Tribe Phyllantheae subtribe Phyllanthinae Pax, Natürl. Pflanzenfam. ed. 1, 3(5): 17. 1890. TYPE: *Phyllanthus* L.

Monoecious or dioecious trees, shrubs, or herbs; branchlets deciduous in some taxa; flowers in axillary glomerules (except *Richeriella*); sepals mostly 4–6, free or connate; stamens 2–15, free or connate; disk extrastaminal and usually dissected (less commonly cupular or absent); anthers introrse or extrorse; pistillode present or absent; pistillate sepals mostly 5 or 6, persistent in fruit; disk usually cupular, often lobed (sometimes dissected); carpels mostly 3 (rarely 2 or 4–10); styles free or connate, bifid or entire; ovules hemitropous; fruit usually capsular (sometimes baccate or drupaceous); seeds usually 2 per locule; testa smooth or sculptured; endosperm copious; cotyledons broader than and 1–2 times longer than the radicle.

A variable subtribe of nine genera with over 1000 species, evidently monophyletic (possibly excluding *Aerisilvaea*, however). The vast majority of the species in genera lacking pistillodes (except for *Margaritaria* and some species of *Phyllanthus*) share a distinctive vegetative specialization: leaves are reduced to scales on main axes and are developed only on lateral deciduous floriferous axes. This has been designated as "phyllanthoid branching" (Webster, 1956).

KEY TO THE GENERA OF SUBTRIBE FLUEGGEINAE

1a. Pistillode present in staminate flower (sometimes minute).
  2a. Dioecious; stamens 3–7; pistillate calyx not accrescent.
    3a. Flowers in axillary clusters; staminate flowers distinctly pedicellate; seeds mostly 2 per locule ——— 25. *Flueggea*
    3b. Flowers in axillary or cauliflorous racemes or panicles; staminate flowers subsessile; seeds mostly 1 per locule ——— 26. *Richeriella*
  2b. Monoecious; stamens 17–21; pistillate calyx accrescent ——— 27. *Aerisilvaea*
1b. Pistillode absent; monoecious or dioecious.
  4a. Seed coat with bony endotesta (not ventrally invaginated) and fleshy exotesta; fruits dry, irregularly dehiscent; disk annular in both staminate and pistillate flowers; dioecious shrubs or trees ——— 28. *Margaritaria*
  4b. Seed coat lacking bony endotesta and fleshy exotesta (or else endotesta usually ventrally invaginated); fruits, when capsular, usually regularly septicidal; disk usually dissected or absent in staminate flower; monoecious or dioecious trees, shrubs, or herbs.
    5a. Floral disk usually present; seeds dry, not ventrally invaginated.
      6a. Staminate disk extrastaminal; stamens various, but rarely 2 and introrse; cotyledons much broader than radicle ——— 29. *Phyllanthus*
      6b. Staminate disk lobed, intrastaminal; stamens 2, anthers introrse; cotyledons scarcely broader than radicle ——— 30. *Reverchonia*
    5b. Floral disk absent or completely adnate to calyx; pollen grains stephanocolporate; styles bifid or entire; seeds with thickened dry or fleshy exotesta, and usually ventrally invaginated.
      7a. Styles bifid or emarginate; anthers not apiculate; ovary 3-locular.
        8a. Seed-coat dry; staminate calyx ± discoid, not turbinate ——— 31. *Sauropus*
        8b. Seed-coat fleshy; staminate calyx turbinate ——— 32. *Breynia*
      7b. Styles usually entire; anthers apiculate; seed-coat usually fleshy; ovary 3–8-locular ——— 33. *Glochidion*

25. Flueggea Willdenow, Sp. Pl. 4: 637. 1806; Bentham, Gen. Pl. 3: 276. 1880; Webster, Allertonia 3: 273. 1984; Hayden, Brittonia 39: 268. 1987. TYPE: *Flueggea leucopyrus* Willd.

Acidoton P. Browne, Civ. Nat. Hist. Jamaica 335. 1756 (nom. rej.; non *Acidoton* Sw., 1788). TYPE: *Adelia acidoton* L. [= *Flueggea acidoton* (L.) Webster].

Bessera Sprengel, Pl. Minus Cogn. Pugillus 2: 90. 1815. TYPE: *Bessera inermis* Sprengel [prob. = *Flueggea virosa* (Roxb. ex Willd.) Voigt].

Geblera Fischer & Meyer, Index Sem. Hort. Petropol. 1: 28. 1835. TYPE: *Geblera suffruticosa* (Pallas) Fischer & Meyer [= *Flueggea suffruticosa* (Pallas) Baillon].

Colmeiroa Reuter, Bibliot. Univers. Genève 38: 215. 1842. TYPE: *Colmeiroa buxifolia* Reuter [= *Flueggea tinctoria* (L. in Loefl.) Webster].

Pleiostemon Sonder, Linnaea 23: 135. 1850. TYPE: *Pleiostemon verrucosum* (Thunb.) Sonder [= *Flueggea verrucosa* (Thunb.) Webster].

Neowawraea Rock, Indig. Trees Haw. I. 243. 1913. TYPE: *Neowawraea phyllanthoides* Rock [= *Flueggea neowawraea* Hayden].

A genus of 14 species, widespread in the tropics and temperate eastern Asia, but with a disjunct relict distribution. The genus was merged with *Securinega* by Mueller (1866), who was followed by many subsequent workers. However, Baillon (1858), Bentham (1880), and J. D. Hooker (1887) maintained *Flueggea* as distinct; and indeed it is not closely related to *Securinega*, as indicated by both pollen and seed characters.

26. Richeriella Pax & Hoffmann, Pflanzenr. 147. XV (Heft 81): 26. 1922; Natürl. Pflanzenfam. ed. 2, 19c: 48. 1931; Henderson, Garden Bull. Str. Settlem. 7: 122, t. 32. 1933; Airy Shaw, Kew Bull. 25: 489. 1971. TYPE: *Richeriella gracilis* (Merr.) Pax & Hoffm. [*Baccaurea gracilis* Merr.].

A genus of two species native to southern China, the Philippines, Malaya, and Borneo. It is very close to *Flueggea*.

27. Aerisilvaea Radcliffe-Smith, Kew Bull. 45: 149. 1990; 47: 677. 1992. TYPE: *Aerisilvaea sylvestris* Radcliffe-Smith.

A genus of two species, one from Tanzania and the other from Malawi. It is anomalous within this subtribe because of its high stamen number, and its placement must be regarded as provisional until the pollen can be examined. Levin (pers. comm.) suggested that it may be referable to the Drypeteae.

28. Margaritaria L. f., Suppl. Pl. 66. 1781; Airy Shaw, Kew Bull. 20: 386. 1966; Fosberg, Kew Bull. 33: 185. 1978; Webster, J. Arnold Arbor. 60: 407. 1979; Airy Shaw, Kew Bull. 35: 657. 1980; Radcliffe-Smith, Kew Bull. 36: 219. 1981; Fl. Trop. E. Afr. Euphorb. 63. 1987. TYPE: *Margaritaria nobilis* L. f.

Prosorus Dalz., J. Bot. Kew Misc. 4: 345. 1852. TYPE: *Prosorus indicus* Dalz. [= *Margaritaria indica* (Dalz.) Airy Shaw].

Zygospermum Thw. ex Baillon, Etude Gén. Euphorb. 620. 1858. TYPE: *Zygospermum zeylanicum* Thw. ex Baillon [= *Margaritaria cyanosperma* (Gaertner) Airy Shaw].

Wurtzia Baillon, Adansonia I. 1: 186. 1861. TYPE: *Wurtzia tetracocca* Baillon [= *Margaritaria tetracocca* (Baillon) Webster].

Calococcus Kurz ex Teijsm. & Binn., Nat. Tijdschr. Ned. Ind. 27: 48. 1864. TYPE: *Calococcus sundaicus* Kurz ex Teisjm. & Binn. [= *Margaritaria indica* (Dalz.) Airy Shaw].

A genus of 14 species occurring in tropical America, Africa, Asia, and Australia.

29. Phyllanthus L., Sp. Pl. 981. 1753; Gen. Pl. ed. 5, 422. 1754; Baillon, Adansonia I. 1: 24. 1860; Muell. Arg., DC. Prodr. 15(2): 274. 1866; Bentham, Gen. Pl. 3(1): 272. 1880; Hutchinson, Fl. Trop. Afr. 6(1): 692. 1912; Beille, Fl. Indochine 5: 571. 1927; Pax & Hoffm., Natürl. Pflanzenfam. ed. 2, 19c: 60. 1931; Webster, J. Arnold Arbor. 48: 332. 1967; Brittonia 22: 44. 1970; Webster & Airy Shaw, Kew Bull. 26: 85. 1971; Brunel & Roux, Willdenowia 11: 69. 1981; Bull. Mus. Hist. Nat. IV. 3B: 185. 1981; Nordic J. Bot. 4: 469. 1984; Radcliffe-Smith, Fl. Trop. E. Afr. Euphorb. 9. 1987; Rossignol et al., Amer. J. Bot. 74: 1853. 1987; Santiago, Bradea 5(2): 44. 1988; Lebrun & Stork, Enum. Pl. Afr. Trop. 1: 232. 1991; Schmid, Fl. Nouv.-Caléd. 14(2): 31. 1991. TYPE: *Phyllanthus niruri* L. [lectotype, designated by Small in Britton & Brown, Ill. Fl. N. U.S. ed. 2, 2: 453. 1913].

Niruri Adanson, Fam. Pl. 2: 356. 1763. TYPE: *Phyllanthus niruri* L. [lectotype, selected here].

Cicca L., Syst. Nat. ed. 12, 2: 621. 1767. TYPE: *Cicca disticha* L. [= *Phyllanthus acidus* (L.) Skeels].

Xylophylla L., Mant. Alt. 147, 221. 1771. TYPE: *Xylophylla latifolia* L. [= *Phyllanthus epiphyllanthus* L; lectotype].

Conami Aublet, Hist. Pl. Guiane Fr. 926. 1775. TYPE: *Conami brasiliensis* Aubl. [= *Phyllanthus brasiliensis* (Aubl.) Muell. Arg.].

Genesiphylla L'Herit., Sert. Angl. 29. 1778. TYPE: *Genesiphylla asplenifolia* L'Herit. [= *Phyllanthus latifolius* Sw.].

Cathetus Loureiro, Fl. Cochinch. 607. 1790. TYPE: *Cathetus fasciculata* Lour. [= *Phyllanthus cochinchinensis* Spreng.].

Nymphanthus Loureiro, Fl. Cochinch. 543. 1790. TYPE: *Nymphanthus ruber* Lour. [= *Phyllanthus ruber* (Lour.) Spreng.].

Emblica Gaertner, Fruct. Sem. Pl. 2: 122. 1790. TYPE: *Emblica officinalis* Gaertner [= *Phyllanthus emblica* L.].

Kirganelia Juss., Gen. Pl. 387. 1789. TYPE: *Kirganelia virginea* J. F. Gmelin [= *Phyllanthus virgineus* (Gmel.) Pers.].

Tricarium Loureiro, Fl. Cochinch. 557. 1790. TYPE: *Tricarium cochinchinense* Lour. [= *Phyllanthus acidus* (L.) Skeels].

Epistylium Swartz, Fl. Ind. Occ. 2: 1095. 1800. TYPE: *Epistylium axillare* (Sw.) Sw. [= *Phyllanthus axillaris* (Sw.) Muell. Arg.; lectotype].

Geminaria Rafinesque, Western Minerva 42. 1821. TYPE: *Geminaria obovata* Raf. [= *Phyllanthus caroliniensis* Walt.].

Menarda Commerson ex A. Jussieu, Euphorb. Tent. 23, 109. 1824. TYPE: *Menarda cryptophila* Comm. ex A. Juss. [= *Phyllanthus cryptophilus* (Comm. ex A. Juss.) Muell. Arg.].

Anisonema A. Jussieu, Euphorb. Tent. 19. 1824 (nom. rej.). TYPE: *Anisonema reticulatum* (Poir.) A. Juss. [= *Phyllanthus reticulatus* Poir.].

Scepasma Blume, Bijdr. Fl. Jav. 582. 1825. TYPE: *Scepasma buxifolia* Bl. [= *Phyllanthus buxifolius* (Bl.) Muell. Arg.].

Synexemia Rafinesque, Neogenyton 2. 1825. TYPE: *Synexemia caroliniana* Raf. [= *Phyllanthus caroliniensis* Walt.; lectotype].

Hexadena Rafinesque, Sylva Tell. 92. 1838. TYPE: *Hexadena angustifolia* (Sw.) Raf. [= *Phyllanthus angustifolius* (Sw.) Sw.].

Moeroris Rafinesque, Sylva Tell. 91. 1838. TYPE: *Moeroris stipulata* Raf. [= *Phyllanthus stipulatus* (Raf.) Webster].

Nellica Rafinesque, Sylva Tell. 92. 1838. TYPE: *Nellica maderaspatensis* (L.) Raf. ["*maderaspatana*" = *Phyllanthus maderaspatensis* L.].

Asterandra Klotzsch, Arch. Naturgesch. 7(1): 200. 1841. TYPE: *Asterandra cornifolia* (HBK) Kl. [= *Phyllanthus cornifolius* HBK].

Eriococcus Hasskarl, Tijdschr. Natuurl. Gesch. Physiol. 10: 143. 1843. TYPE: *Eriococcus gracilis* Hassk. [= *Phyllanthus gracilipes* Muell. Arg.].

Ceramanthus Hasskarl, Cat. Pl. Hort. Bogor. Alt. 240. 1844. TYPE: *Ceramanthus gracilis* Hassk. [= *Phyllanthus albidiscus* (Ridley) Airy Shaw].

Macraea Wight, Icon. Pl. Ind. Or. 5(2): 27, t. 1901, 1902. 1852 (non *Macraea* Lindley, 1828). TYPE: *Macraea oblongifolia* Wight [= *Phyllanthus simplex* Retz.; lectotype].

Reidia Wight, Icon. Pl. Ind. Or. 5(2): 27, t. 1903, 1904. 1852. TYPE: *Reidia floribunda* Wight [= *Phyllanthus wightianus* Muell. Arg.; lectotype chosen here].

Chorisandra Wight, Icon. Pl. Ind. Or. 6: 13, t. 1994. 1853. TYPE: *Chorisandra pinnata* Wight [= *Phyllanthus pinnatus* (Wight) Webster].

Dichelactina Hance, Walp. Ann. Bot. Syst. 3: 375. 1852. TYPE: *Dichelactina nodicaulis* Hance [= *Phyllanthus acidus* (L.) Skeels].

Staurothyrax Griffith, Notul. Pl. Asiat. 4: 476. 1854. TYPE: not designated [ex descr., = *Phyllanthus acidus* (L.) Skeels].

Hemicicca Baillon, Etude Gén. Euphorb. 645. 1858. TYPE: *Hemicicca japonica* Baillon [= *Phyllanthus flexuosus* (Sieb. & Zucc.) Muell. Arg.].

Williamia Baillon, Etude Gén. Euphorb. 559. 1858. TYPE: *Williamia pruinosa* Baill. [= *Phyllanthus discolor* Poepp. ex Spr.].

Orbicularia Baillon, Etude Gén. Euphorb. 616. 1858. TYPE: *Orbicularia phyllanthoides* Baillon [nom. illeg., = *Phyllanthus orbicularis* HBK].

Phyllanthodendron Hemsley, Hook. Ic. Pl. 26: t. 2563, 2564. 1898. TYPE: *Phyllanthodendron mirabilis* (Muell. Arg.) Hemsl. [= *Phyllanthus mirabilis* Muell. Arg.].

Aporosella Chodat, Bull. Herb. Boiss. II. 5: 488. 1905. TYPE: *Aporosella hassleriana* Chod. [= *Phyllanthus chacoensis* Morong].

Flueggeopsis (Muell. Arg.) K. Schumann, Fl. Deutsche Schutzgeb. Nachtr. 289. 1905. TYPE: *Phyllanthus glaucus* Muell. Arg.

Nymania K. Schumann, Fl. Deutsche Schutzgeb. Nachtr. 291. 1905. TYPE: *Nymania insignis* K. Schum. [= *Phyllanthus schumannianus* L. S. Smith].

Uranthera Pax & Hoffm., Pflanzenr. 147. III (Heft 47): 95. 1911. TYPE: *Uranthera siamensis* Pax & Hoffm. [= *Phyllanthus roseus* (Craib & Hutch.) Beille].

Dimorphocladium Britton, Mem. Torrey Bot. Club 16: 74. 1920. TYPE: *Dimorphocladium formosum* (Urb.) Britton [= *Phyllanthus formosus* Urb.].

Ramsdenia Britton, Mem. Torrey Bot. Club 16: 72. 1920. TYPE: *Ramsdenia incrustata* (Urb.) Britton [= *Phyllanthus incrustatus* Urb.].

Roigia Britton, Mem. Torrey Bot. Club 16: 73. 1920. TYPE: *Roigia comosa* (Urb.) Britton [= *Phyllanthus comosus* Urb.].

Dendrophyllanthus Spencer Moore, J. Linn. Soc. Bot. 45: 395. 1921. TYPE: *Dendrophyllanthus comptonii* Sp. Moore [= *Phyllanthus moorei* Schmid].

Pseudoglochidion Gamble, Kew Bull. 1925: 329. 1925. TYPE: *Pseudoglochidion anamalayanum* Gamble [= **Phyllanthus anamalayanus** (Gamble) Webster, comb. nov.].

Hexaspermum Domin, Bibl. Bot. 89: 315. 1927. TYPE: *Hexaspermum paniculatum* Domin [= *Phyllanthus clamboides* (F. Muell.) Diels].

Arachnodes Gagnepain, Notul. Syst. (Paris) 14: 32. 1950; Airy Shaw, Kew Bull. 14: 469. 1960. TYPE: *Arachnodes chevalieri* Gagnep., loc. cit. [= **Phyllanthus chevalieri** (Gagnep.) Webster, comb. nov.].

A large and very diverse genus of 750–800 species, about 200 of which are American, 100 African, 70 Madagascan, and the remainder Asian and Australasian. Many attempts have been made to subdivide the genus, which very possibly is unnatural. Here, the broad concept of Mueller (1866) has been modified by the recognition of *Glochidion* and *Margaritaria* as distinct.

30. Reverchonia A. Gray, Proc. Amer. Acad. Arts Sci. 16: 107. 1880; Webster & Miller, Rhodora 65: 200. 1963. TYPE: *Reverchonia arenaria* A. Gray.

A monotypic genus confined to sand dunes in the southwestern United States and adjacent Mex-

ico. Although it is very close to *Phyllanthus*, it would appear excessively foreign if placed in that genus.

31. Sauropus Blume, Bijdr. 595. 1826; Muell. Agr., DC. Prodr. 15(2): 239. 1866; Bentham, Gen. Pl. 3: 271. 1880; Pax & Hoffm., Pflanzenr. 147. XV (Heft 81): 215. 1922; Airy Shaw, Kew Bull. 23: 42. 1969; Kew Bull. 35: 669. 1980. TYPE: *Sauropus albicans* (L.) Blume [= *Sauropus androgynus* (L.) Merr.; lectotype, selected here].

Ceratogynum Wight, Icon. Pl. Or. 5(2): 26. 1852. TYPE: *Ceratogynum rhamnoides* Wight [= *Sauropus quadrangularis* (Willd.) Muell. Arg.].

Diplomorpha Griffith, Notul. Pl. Asiat. 4: 479. 1854. TYPE: *Diplomorpha herbacea* Griffith [= *Sauropus bacciformis* (L.) Airy Shaw].

Synostemon F. Muell., Fragm. Phyt. Austral. 1: 32. 1858. TYPE: *Synostemon ramosissimus* F. Muell. [= *Sauropus ramosissimus* (F. Muell.) Airy Shaw; lectotype, designated by Wheeler, 1975].

Breyniopsis Beille, Bull. Soc. Bot. France 72: 157. 1925. TYPE: *Breyniopsis pierrei* Beille [= **Sauropus pierrei** (Beille) Webster, comb. nov.].

Heterocalymnantha Domin, Bibl. Bot. 89: 313. 1927. TYPE: *Heterocalymnantha minutifolia* Domin [= *Sauropus rigens* (F. Muell.) Airy Shaw].

A genus of about 50 species distributed from India and Sri Lanka to southern China, the Philippines, Borneo, and Australia. Airy Shaw (1980) has transferred a large number of Australian species of *Synostemon* to *Sauropus*, and it appears he may have good reason to do so, although the demarcation of *Sauropus* from *Breynia* is almost as problematical as its separation from *Synostemon*.

32. Breynia J. R. & G. Forster, Char. Gen. Pl. 145. 1776 (nom. cons.); Muell. Arg., DC. Prodr. 15(2): 438. 1866; Bentham, Gen. Pl. 3: 277. 1880; Hook f., Fl. Brit. Ind. 5: 329. 1887; Beille, Fl. Indochine 5: 631. 1927; Pax & Hoffm., Natürl. Pflanzenfam. ed. 2, 19c: 59. 1931. *Foersteria* Scopoli, Intr. Hist. Nat. 98. 1777. TYPE: *Breynia disticha* J. R. & G. Forster.

Melanthesa Blume, Bijdr. 590. 1826. TYPE: *Melanthesa racemosa* Blume [lectotype, selected here; = *Breynia racemosa* (Blume) Muell. Arg.].

Melanthesopsis Muell. Arg., Linnaea 32: 74. 1863. TYPE: *Melanthesopsis lucens* (Poir.) Muell. Arg. [= *Breynia fruticosa* (L.) Hook. f.; lectotype, designated by Wheeler, 1975].

A difficult genus of 10–15 highly variable species, found in tropical eastern Asia, Indonesia, tropical Asia, and the Pacific islands. The genus is barely separable from *Sauropus* on the one hand, and *Glochidion* on the other.

33. Glochidion J. R. & G. Forster, Char. Gen. Pl. 113, t. 57. 1776 (nom. cons.); Muell. Arg., Flora 1865: 369. 1865; Hook. f., Fl. Brit. Ind. 5: 305. 1887; Beille, Fl. Indochine 5: 608. 1927; Alston, Ann. Roy. Bot. Gard. Peradeniya 11: 1. 1928; Pax & Hoffm., Natürl. Pflanzenfam. ed. 2, 19c: 56. 1931; Airy Shaw, Kew Bull. Add. Ser. 4: 115. 1975; Kew Bull. Add. Ser. 8: 92. 1980; Kew Bull. 35: 633. 1980; 36: 298. 1981; A. C. Smith, Fl. Vitiensis Nova 2: 467. 1981. TYPE: *Glochidion ramiflorum* J. R. & G. Forster.

Agyneia L., Mantissa Pl. 2: 161. 1771. TYPE: *Agyneja pubera* L. [= *Glochidion puberum* (L.) Muell. Arg.; lectotype, selected here].

Bradleja Banks ex Gaertner, Fruct. Sem. Pl. 2: 127. 1790. TYPE: *Bradleja sinica* Gaertner [= *Glochidion sinicum* (Gaertner) H. & A.].

Gynoon A. Juss., Mém. Mus. Hist. Nat. Paris 10: 335. 1823. TYPE: *Gynoon rigidum* A. Juss. [= *Glochidion rigidum* (A. Juss.) Muell. Arg.].

Glochidionopsis Blume, Bijdr. 588. 1826. TYPE: *Glochidionopsis sericea* Blume [= *Glochidion sericeum* (Blume) Hook. f.].

Glochisandra Wight, Icon. Pl. Ind. Or. 5: 26. 1852. TYPE: *Glochisandra acuminata* Wight [= *Glochidion lanceolarium* (Roxb.) Dalz.].

Zarcoa Llanos, Bot. Zeit. 15: 423. 1857. TYPE: *Zarcoa philippica* Llanos [= *Glochidion album* (Blanco) Boerl.].

Coccoglochidion K. Schum., Nachtr. Fl. Schutzgeb. 292. 1905. TYPE: *Coccoglochidion ethryococcus* [= *Glochidion philippicum* (Cav.) C. B. Robinson].

Hemiglochidion (Muell. Arg.) K. Schum., Nachtr. Fl. Schutzgeb. 289. 1905. TYPE: *Glochidion ramiflorum* Forst. [lectotype, designated by Wheeler, 1975; the choice of *Hemiglochidion hylodendron* K. Schum. as lectotype by Farr et al. (1979) appears invalid, as the species was not included in *Glochidion* sect. *Hemiglochidion* by Mueller].

Tetraglochidion K. Schum., Nachtr. Fl. Schutzgeb. 291. 1905. TYPE: *Tetraglochidion gimi* K. Schum. [= *Glochidion gimi* (K. Schum.) Pax & Hoffm.].

An Asian and Australasian genus of more than 200 species, a few extending to Polynesia. The genus was combined with *Phyllanthus* by Mueller (1866) and Bentham (1880), but most subsequent workers have treated it as distinct, even though it represents a specialized offshoot from ancestral taxa within *Phyllanthus*.

Tribe 5. DRYPETEAE (Grisebach) Hurusawa, J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 6: 334. 1954 (as tribe in Antidesmataceae). Phyllan-

theae subtribe Drypeteae Griseb., Fl. Br. W. Ind. 31. 1859. TYPE: *Drypetes* Vahl.

Antidesmeae * Putranjiveae Endl., Gen. Pl. 287. 1837. Ordo Putranjiveae Endlicher, Gen. Pl. Ord. Nat. 287. 1837. Putranjivaceae Endl. ex Meeuse, Euphorbiaceae Auct. Plur. 30. 1990. TYPE: *Putranjiva* Wallich.

Cyclostemonées Baillon, Etude Gén. Euphorb. 561. 1858. Phyllantheae subtribe Cyclostemoneae Baillon ex Muell. Arg., Linnaea 34: 64. 1865. TYPE: *Cyclostemon* Blume [= *Drypetes* Vahl].

Dioecious trees or shrubs; leaves entire or dentate, stipulate; flowers in axillary clusters, or cauliflorous; sepals mostly 4 or 5, imbricate; petals absent; staminate disk intrastaminal; stamens (2–) 3–20(–50), free, anthers introrse or extrorse; pollen grains 3-colporate, reticulate; pistillode small or obsolete; pistillate sepals deciduous (persistent in *Sibangea*); disk annular or lacking; ovary usually 1- or 2-locular; styles mostly entire and dilated; ovules anatropous, with massive obturator; fruit capsular or drupaceous; seeds 1 per locule or fruit; endosperm copious; cotyledons plane, broader and somewhat longer than radicle.

As circumscribed here, tribe Drypeteae includes four genera, with the vast majority of species in the large and variable genus *Drypetes*. The recent study by Hayden has demonstrated that *Neowawraea*, included in the Drypeteae by Webster (1975), is really a species of *Flueggea*.

KEY TO THE GENERA OF TRIBE DRYPETEAE

1a. Ovary 3-locular; fruit capsular; styles bifid, style-branches slender ..... 34. *Lingelsheimia*
1b. Ovary mostly 1- or 2-locular; fruit drupaceous; styles not bifid.
  2a. Disk present; stamens mostly 4 or more; styles stigmatiform.
    3a. Pistillate sepals imbricate in bud, deciduous in fruit ..... 35. *Drypetes*
    3b. Pistillate sepals open in bud, persistent in fruit ..... 36. *Sibangea*
  2b. Disk absent; stamens mostly 2 or 3; styles petaloid-dilated ..... 37. *Putranjiva*

34. Lingelsheimia Pax, Bot. Jahrb. 43: 317. 1909; Mildbraed, Deutsche Zentral-Afr. Exped. 2: t. 54, 55. 1912; Pax & Hoffm., Pflanzenr. 147. XV (Heft 81): 279. 1922; Léonard, Bull. Soc. Roy. Bot. Belg. 84: 49. 1951; Brenan, Kew Bull. 1952: 445. 1953; Léonard, Bull. Jard. Bot. Brux. 32: 513. 1962. TYPE: *Lingelsheimia frutescens* Pax.

Danguyodrypetes Leandri, Bull. Soc. Bot. France 85: 524. 1938. TYPE: *Danguyodrypetes manongarivensis* Leandri [= **Lingelsheimia manongarivensis** (Leandri) Webster, comb. nov.].

As interpreted by Léonard (1951, 1962b), *Lingelsheimia* is an African genus of two species. However, the four Madagascan species referred to *Danguyodrypetes* by Leandri clearly appear congeneric. The genus appears anomalous in the Drypeteae, and it is possible that its correct place is in tribe Phyllantheae. Levin (pers. comm.) suggests a possible affinity to *Aerisilvaea*.

35. Drypetes Vahl, Eclog. Amer. 3: 49. 1810; Muell. Arg., DC. Prodr. 15(2): 453. 1866; Bentham, Gen. Pl. 3: 278. 1880; Pax & Hoffm., Pflanzenr. 147. XV (Heft 81): 229. 1922; Hurusawa, J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 6: 337. 1954; Leandri, Fl. Madag. 111(1): 144. 1958; van Steenis, Blumea 10: 140. 1960; Léonard, Bull. Jard. Bot. Brux. 32: 513. 1962; Smith & Ayensu, Brittonia 16: 220. 1964; Airy Shaw, Kew Bull. 18: 272. 1965; 27: 309. 1972; Add. Ser. 4: 97. 1975; Kew Bull. 36: 286. 1981; A. C. Smith, Fl. Vitiensis Nova 2: 455. 1981. TYPE: *Drypetes glauca* Vahl.

Koelera Willd., Sp. Pl. ed. 4, 750. 1806, nom. illeg. (non *Koeleria* Pers., 1805). *Limacia* Dietr., Nachr. Vollst. Lex. Gartn. 4: 383. 1818, nom. illeg. (non *Limacia* Lour., 1790). TYPE: *Koelera laurifolia* Willd. [= *Drypetes lateriflora* (Sw.) Kr. & Urb.].

Liparena Poit. ex Leman, Dict. Sci. Nat. 27: 6. 1823. TYPE: not designated.

Cyclostemon Blume, Bijdr. 597. 1826. TYPE: *Cyclostemon macrophyllum* Blume [lectotype, selected here; = *Drypetes macrophylla* (Blume) Pax & Hoffm.].

Hemicyclia Wight & Arn., Edinb. New Phil. J. 14: 297. 1833 (as *Hemicyclia*). TYPE: *Hemicyclia sepiaria* Wight & Arn. [= *Drypetes sepiaria* (Wight & Arn.) Pax & Hoffm.].

Astylis Wight, Icon. Pl. Ind. Orient. 6: t. 1992. 1853. TYPE: *Astylis venusta* Wight [= *Drypetes venusta* (Wight) Pax & Hoffm.].

Sphragidia Thwaites, Hook. J. Bot. Kew Misc. 7: 269. 1855. TYPE: *Sphragidia zeylanica* Thwaites [= *Drypetes longifolia* (Blume) Pax & Hoffm.].

Dodecastemon Hasskarl, Versl. Meded. Afd. Natuurk. Kon. Akad. Wet. 4: 141. 1856. TYPE: *Dodecastemon teysmanii* Hassk. [= *Drypetes teysmanii* (Hassk.) Bakh. f. & van Steenis].

Pycnosandra Blume, Mus. Bot. Lugd.-Bat. 2: 191. 1856. TYPE: *Pycnosandra serrata* (Blume) Blume [= *Drypetes serrata* (Blume) Pax & Hoffm., nom. illeg. (non *D. serrata* (Krug & Urb.) = *Drypetes teysmanii* (Hassk.) Bakh. f. & van Steenis].

Cometia Du Petit Thouars ex Baillon, Etude Gén. Euphorb. 642. 1858. TYPE: *Cometia thouarsii* Baillon [= *Drypetes thouarsii* (Baillon) Leandri].

Anaua Miquel, Fl. Ned. Ind., Eerste Bijv. 410. 1861. TYPE: *Anaua sumatrana* Miq. [= *Drypetes sumatrana* (Miq.) Pax & Hoffm.].

Laneasagum Beddome, Madras J. Lit. Sci., ser. 2, 22: 71. 1861. TYPE: *Laneasagum oblongifolia* Bedd. [= *Drypetes longifolia* (Bl.) Pax & Hoffm.].
Stelechanteria Thouars ex Baillon, Adansonia I. 4: 147. 1864. TYPE: *Stelechanteria thouarsiana* Baillon [= *Drypetes thouarsiana* (Baillon) Capuron].
Freireodendron Muell. Arg., DC. Prodr. 15(2): 245. 1866. TYPE: *Freireodendron sessiliflorum* (Fr. Allem.) Muell. Arg. [= *Drypetes sessiliflora* Fr. Allem.].
Humblotia Baillon, Bull. Mens. Soc. Linn. Paris 1: 593. 1886. TYPE: *Humblotia comorensis* Baillon [= *Drypetes comorensis* (Baillon) Pax & Hoffm.].
Guya Frappier ex Cordemoy, Fl. Ile Réunion 350. 1895. TYPE: *Guya caustica* Frapp. ex Cordem. [= *Drypetes caustica* (Frapp. ex Cordemoy) Airy Shaw].
Riseleya Hemsley, J. Bot. 55: 286. 1917. TYPE: *Riseleya griffithii* (Hook. f.) Hemsl. [= *Drypetes indica* (Muell. Arg.) Pax & Hoffm.].
Calyptosepalum Spencer Moore, J. Bot. 63 (suppl.): 91. 1925. TYPE: *Calyptosepalum sumatranum* Sp. Moore [= *Drypetes calyptosepala* Airy Shaw].
Brexiopsis H. Perrier, Notul. Syst. (Paris) 10: 192. 1942. TYPE: *Brexiopsis aquifolia* H. Perr. [= *Drypetes bathiei* Capuron & Leandri].

A large and variable genus of ca. 200 species; poorly represented in the New World, with ca. 10 species; ca. 60 species in Africa and Madagascar; the remainder in Asia and Australasia. Mueller (1866) and Bentham (1880) recognized *Cyclostemon* and *Hemicyclia* as distinct from *Drypetes*, but most 20th century students have followed Pax & Hoffman (1922) in combining them. There is considerable anatomical and palynological variation within *Drypetes* sensu lato, however, and the generic limits require further study. I am indebted to Geoffrey Levin (pers. comm.) for critical suggestions on the generic synonymy.

36. Sibangea Oliver, Hook. Ic. Pl. 15: 9, t. 1411. 1883; Radcliffe-Smith, Kew Bull. 32: 480. 1978; Fl. Trop. E. Afr., Euphorb. 101. 1987. TYPE: *Sibangea arborescens* Oliver.

As interpreted by Radcliffe-Smith, *Sibangea* includes three African species. The genus is very close to *Drypetes*, and it remains to be seen whether it can be maintained as distinct.

37. Putranjiva Wallich, Tent. Fl. Nepal 61. 1826; Muell. Arg., DC. Prodr. 15(2): 443. 1866; Bentham, Gen. Pl. 3: 277. 1880; Pax & Hoffm., Natürl. Pflanzenfam. ed. 2, 19c: 59. 1931. TYPE: *Putranjiva roxburghii* Wallich [*Nageia putranjiva* Roxburgh].

Palenga Thwaites, Hook. J. Bot. Kew Gard. Misc. 8: 270. 1856. TYPE: *Palenga zeylanica* Thwaites [= *Putranjiva zeylanica* (Thwaites) Muell. Arg.].
Liodendron Keng, J. Washington Acad. Sci. 41: 201. 1951. TYPE: *Liodendron matsumurae* (Koidzumi) Keng [= *Putranjiva matsumurae* Koidz.].

A small genus of three or four Asian species (India, Sri Lanka, Taiwan, and the Ryukyu Islands), questionably separable from *Drypetes*.

Tribe 6. ANTIDESMEAE (Sweet) Hurusawa, J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 6: 322. 1954 [as tribe of Antidesmataceae]. Ordo Stilagineae Agardh, Aphor. 199, Class. Pl. 9. 1825. Ordo Antidesmeae Sweet, Hort. Brit. ed. 2, 460. 1830. Tribe Biovulatae sect. Antidesmeae Thw., Enum. Pl. Zeyl. 289. 1861. TYPE: *Antidesma* L.

Dioecious (rarely monoecious) trees or shrubs (rarely herbs); leaves alternate, entire, pennineved, glandular or eglandular, stipulate; inflorescences usually axillary, amentlike; sepals 3–6, free or connate, imbricate; petals reduced or absent (except *Spondianthus*); disk annular, lobed, or dissected; stamens 2–8, free or nearly so; anthers extrorse or introrse; pollen grains mostly prolate, 3-colporate, reticulate; pistillode present or absent; carpels (1) 2 or 3 (–5); ovules anatropous; styles bifid to bipartite (rarely entire, sometimes dilated); fruit capsular or drupaceous; seeds mostly 1 per locule (or 1 per fruit); seed-coat dry or fleshy; endosperm thin to copious; cotyledons mostly broader than radicle.

This mainly paleotropical tribe of 18 genera in 5 subtribes is well characterized by its leaves with tanniniferous epidermis (Levin, 1986a) and prolate pollen grains with 3 narrow colpi (Köhler, 1965). The tribe is here given a broader circumscription than that of Hurusawa (1954), who did not include the Spondianthinae, Uapacinae, or Porantherinae.

KEY TO THE SUBTRIBES OF TRIBE ANTIDESMEAE

1a. Stems with resinous secretion; inflorescence paniculate, or capitulate.
  2a. Petals present; inflorescence terminal, paniculate, bracts small; pollen sexine not spinulose; fruit capsular; stomata paracytic ..... 6a. Spondianthinae
  2b. Petals absent; inflorescences axillary, capitate, bracts large and involucrate; pollen sexine spinulose; fruit drupaceous; stomata anisocytic ..... 6b. Uapacinae
1b. Stems lacking resin; inflorescence not paniculate or capitulate; petals mostly absent.
  3a. Inflorescences axillary, amentlike; trees or shrubs (except *Cyathogyne*).
    4a. Pollen grains globose or slightly prolate; anther locules not pendulous; leaves sometimes glandular; stomata anisocytic ..... 6c. Scepinae
    4b. Pollen grains distinctly prolate; anther locules ± pendulous; leaves not glandular; stomata paracytic ..... 6d. Antidesminae

3b. Inflorescences terminal, corymbiform; herbs ..... 6e. Porantherinae

Subtribe 6a. SPONDIANTHINAE (Webster) Webster, stat. nov. Tribe Spondiantheae Webster, Taxon 24: 594. 1975. TYPE: *Spondianthus* Engler.

Dioecious trees; leaves entire, penninerved, stipules caducous; inflorescences terminal (at least in part), paniculate, bracts small; flowers (at least the staminate) with petals; staminate disk dissected; stamens 5, filaments free, anthers introrse; pistillode present; pistillate disk lobed; styles free; fruit loculicidally dehiscent; columella persistent; seeds 1 per locule, testa dry; endosperm scanty; embryo with cotyledons much broader than radicle.

A monotypic tribe, including only the African genus *Spondianthus*. Pax & Hoffmann (1922) placed it adjacent to *Thecacoris*, a genus of subtribe Antidesminae. Levin (1986c), on the basis of foliar characters, suggested that it is the primitive sister group of the other woody tribes of Antidesmeae. The observations of Köhler (1965) on pollen suggest a similar position.

38. Spondianthus Engler, Bot. Jahrb. 36: 215. 1905; Hutch., Hook. Icon. Pl. 30: t. 2986. 1911; Fl. Trop. Afr. 6(1): 1044. 1913; Pax & Hoffm., Pflanzenr. 147. XV (Heft 81): 13. 1922; Keay, Fl. W. Trop. Afr. ed. 2, 1: 372. 1958; Aubreville, Fl. Forest. Côte d'Ivoire, ed. 2, 2: 62. 1959; Radcliffe-Smith, Fl. E. Trop. Afr. Euphorb. 104. 1987; Léonard & Nkounkou, Bull. Jard. Bot. Nat. Belg. 59: 133. 1989. TYPE: *Spondianthus preussii* Engler.

Megabaria De Wild., Etud. Fl. Bas & Moy. Congo 2: 284. 1908. TYPE: *Megabaria trillesii* De Wild. [= *Spondianthus preussii* Engler].

A monotypic genus of a single variable species, widespread in tropical Africa from Liberia to Angola and Tanzania.

Subtribe 6b. UAPACINAE Muell. Arg., Linnaea 34: 64. 1865 (as Phyllantheae subtr. Uapaceae). Tribe Uapaceae (Muell. Arg.) Hutch., Amer. J. Bot. 56: 747. 1969. Family Uapaceae (Muell. Arg.) Airy Shaw, Kew Bull. 18: 270. 1965. TYPE: *Uapaca* Baillon.

Dioecious trees or shrubs; leaves entire, pinnately veined, stipules caducous; inflorescences axillary, capitate, involucrate, pedunculate; flowers apetalous and without floral disk; calyx gamophyllous; stamens 5, filaments free, anthers introrse; pistillode apically dilated; pistillate calyx gamophyllous; ovary mostly 3-locular; styles free, multifid; fruit drupaceous; seeds 1 per locule, albuminous; cotyledons much longer than radicle.

This subtribe includes only the single genus *Uapaca*, which has always appeared isolated because of its remarkable involucrate inflorescences: Airy Shaw (1965) and Meeuse (1990) have assigned it to a separate family, Uapacaceae. However, Bentham (1880) juxtaposed it with *Aporusa*, and Pax (1890) referred it to his subtribe Antidesminae. Those intuitions appear confirmed by the foliar anatomical studies of Levin (1986a, b, c), who has found that the tanniniferous epidermal cells and anisocytic stomata indicate an affinity with subtribe Scepinae. On the other hand, the distinctive pollen and resiniferous stems of *Uapaca* are divergent characters, and it appears best referred to a separate subtribe.

39. Uapaca Baillon, Etude Gén. Euphorb. 595. 1858; Muell. Arg., DC. Prodr. 15(2): 489. 1866; Pax & Hoffm., Pflanzenr. 147. XV (Heft 81): 298. 1922; Leandri, Fl. Madag. 111(1): 163. 1958; Radcliffe-Smith, Fl. E. Trop. Afr., Euphorb. 567. 1988. TYPE: *Uapaca thouarsii* Baillon [lectotype, selected by Airy-Shaw, Kew Bull. 18: 271. 1965].

A genus of ca. 60 species in Africa and Madagascar.

Subtribe 6c. SCEPINAE (Lindley) Webster, stat. nov. Ordo Scepaceae Lindl., Nat. Syst. Bot. ed. 2, 171. 1836. TYPE: *Scepa* Lindl. [= *Aporusa* Bl.].

Ordo Aporuseae Lindl. ex Miq., Fl. Ind. Bat. 1(2): 430. 1858. Tribe Aporuseae (Lindl. ex Miq.) Airy Shaw, Hook. Icon. Pl. 38: t. 3701. 1974; Webster, Taxon 24: 594. 1975. TYPE: *Aporusa* Bl.

Dioecious or monoecious trees or shrubs, stems without resinous secretion; leaves often with laminar glands, stomata mostly anisocytic (paracytic in *Jablonskia*), stipules deciduous or persistent; staminate bracts mostly each with 3 or more flowers; sepals 4–8, free; petals absent; disk lobed, dissected, or absent; stamens 4–8, free; anthers dehiscing longitudinally, connective not enlarged; pollen grains subglobose to subprolate, 3-colporate, reticulate or tectate; pistillode present; ovary 2–5-locular; styles bifid or unlobed; fruit capsular or tardily dehiscent and subdrupaceous; seeds 1–6 per fruit, seed-coat dry or fleshy; endosperm thin

to copious, cotyledons mostly distinctly broader and longer than radicle.

This taxon, although early designated by Lindley (1836) as an "ordo," was confounded by Mueller (1866) and later authors with the Antidesminae, and was first recognized in the 20th century by Airy Shaw (1974) at the tribal rank. Since Lindley published the Scepaceae over 20 years before the ordo Aporuseae was proposed, it seems preferable to preserve his name. The seven genera of Scepinae are scattered through the tropics in America, Africa, and Asia, with only *Baccaurea* attaining the Pacific islands.

KEY TO THE GENERA OF SUBTRIBE SCEPINAE

1a. Pistillate disk dissected; styles dilated, entire to slightly lobed ..... 40. *Protomegabaria*
1b. Pistillate disk cupular or absent.
  2a. Staminate disk present.
    3a. Pistillate disk present; pistillate sepals persistent in fruit.
      4a. Dioecious; flowers racemose; stipules deciduous.
        5a. Capsule loculicidal; staminate flowers mostly one per bract ..... 41. *Maesobotrya*
        5b. Capsule septicidal; staminate flowers several per bract ..... 42. *Richeria*
      4b. Monoecious; flowers in axillary glomerules; stipules persistent; capsule septicidal ..... 43. *Jablonskia*
    3b. Pistillate disk absent; pistillate sepals deciduous.
      6a. Dioecious; styles bifid ..... 44. *Baccaurea*
      6b. Monoecious; styles unlobed ..... 45. *Apodiscus*
  2b. Staminate disk absent.
    7a. Pistillode massive, peltate; stamens 5 or 6; carpels mostly 3 or 4; styles stigmatiform ..... 46. *Ashtonia*
    7b. Pistillode small; stamens mostly 2 (rarely 3–5); carpels mostly 2 (rarely 3 or 4); styles bifid ..... 47. *Aporusa*

40. Protomegabaria Hutchinson, Hook. Icon. Pl. 30: t. 2929. 1911; Fl. Trop. Afr. 6(1): 656. 1912; Pax & Hoffm., Pflanzenr. 147. XV (Heft 81): 43. 1922; Keay, Fl. W. Trop. Afr. ed. 2, 1: 373. 1958; Aubreville, Fl. For. Côte, d'Ivoire 2: 68, t. 147. 1959. TYPE: *Protomegabaria stapfiana* (Beille) Hutch. (lectotype, selected here).

Two species of West Africa.

41. Maesobotrya Bentham, Hook. Icon. Pl. 13: 75, t. 1296. 1879; Gen. Pl. 3: 284. 1880; Hutchinson, Fl. Trop. Afr. 6(1): 663. 1912; Pax & Hoffm., Pflanzenr. 147. XV (Heft 81): 17. 1922; Léonard, Bull. Jard. Bot. Brux. 17: 256. 1945; Keay, Fl. W. Trop. Afr. ed. 2, 1: 373. 1958; Radcliffe-Smith, Fl. Trop. E. Afr. Euphorb. 112. 1987. TYPE: *Maesobotrya floribunda* Bentham.

Staphysora Pierre, Bull. Soc. Linn. Paris 1233. 1896; Pax, Bot. Jahrb. 23: 521. 1897. TYPE: *Staphysora dusenii* Pax [= *Maesobotrya dusenii* (Pax) Hutch.].

An African genus of ca. 20 species, all in West Africa and only 1 species extending east to Uganda. The genus is extremely close to the neotropical *Richeria*.

42. Richeria Vahl, Eclog. Amer. 1: 30, t. 4. 1797; Muell. Arg., DC. Prodr. 15(2): 466. 1866; Fl. Bras. 11(2): 13. 1873; Bentham, Genera Plantarum 3: 286. 1880; Pax & Hoffm., Pflanzenr. 147. XV (Heft 81): 26. 1922; Jablonski, Mem. New York Bot. Gard. 17: 124. 1967; Philcox, Fl. Trin. Tob. 2(9): 638. 1979; Webster, Ann. Missouri Bot. Gard. 75: 1093. 1989; Secco & Webster, Bol. Mus. Para. Emilio Goeldi, Bot. 6: 141–158. 1990. TYPE: *Richeria grandis* Vahl.

Guarania Weddell ex Baillon, Etude Gén. Euphorb. 598. 1858. TYPE: *Guarania gardneriana* Baillon [= *Richeria gardneriana* (Baillon) Baillon; lectotype].

A genus of several poorly defined taxa, treated as two species by Secco & Webster (1990); extending in lowland and montane tropical rainforest from Costa Rica and the Lesser Antilles to Peru and Brazil.

43. Jablonskia Webster, Syst. Bot. 9: 232. 1984. TYPE: *Jablonskia congesta* (Benth. ex Muell. Arg.) Webster [*Securinega congesta* Benth. ex Muell. Arg.].

Monotypic, the single species confined to Amazonian South America. The genus is isolated in subtribe Scepinae by its distinctive pollen type and paracytic stomata and shows some similarities to *Celianella* Jabl. in subtribe Antidesminae. Its placement requires further evaluation.

44. Baccaurea Loureiro, Fl. Cochinch. 661. 1790; Muell. Arg., Prodr. 15(2): 456. 1866; Bentham, Gen. Pl. 3: 283. 1880; Pax & Hoffm., Pflanzenr. 147. XV (Heft 81): 45. 1922; Airy Shaw, Kew Bull. 14: 353. 1960; Backer & Bakh., Fl. Java 1: 453. 1963; Whitmore, Tree Fl. Malaya 2: 63. 1973; A. C. Smith, Fl. Vit. Nov. 2: 450. 1981; Thin, Công Trình Nghiên Cú'u Khoa Hoc 10: 78. 1986. TYPE: *Baccaurea ramiflora* Lour. [lectotype, selected by Merrill, 1935].

Pierardia Roxb. ex Jack, Trans. Linn. Soc. London 14: 119. 1823. TYPE: *Pierardia dulcis* Jack [= *Baccaurea dulcis* (Jack) Muell. Arg.].

Adenocrepis Blume, Bijdr. 579. 1825. TYPE: *Adenocrepis javanica* Bl. [= *Baccaurea javanica* (Bl.) Muell. Arg.].

Calyptroon Miquel, Fl. Ned. Ind., Erste Bijv. 471. 1861. TYPE: *Calyptroon sumatranum* Miq. [= *Baccaurea sumatrana* (Miq.) Muell. Arg.].

Microsepala Miquel, Fl. Ned. Ind., Erste Bijv. 444. 1861. TYPE: *Microsepala acuminata* Miq. [= *Baccaurea javanica* (Bl.) Muell. Arg.].

Everettiodendron Merrill, Phil. J. Sci. Bot. 4: 279. 1909. TYPE: *Everettiodendron philippinense* Merr. [= *Baccaurea philippinensis* (Merr.) Merr.].

Gatnaia Gagnepain, Bull. Soc. Bot. France 71: 870. 1924. TYPE: *Gatnaia annamica* Gagnep. [= *Baccaurea oxycarpa* Gagnep.].

A diversified genus of ca. 75 paleotropical species, extending from India to the Philippines, New Guinea, and the Pacific islands.

45. Apodiscus Hutchinson, Bull. Soc. Bot. France 58, Mem. 8: 205. 1912; Fl. Trop. Afr. 6(1): 1045. 1913; Hook. Icon. Pl. 31: t. 3032. 1915; Pax & Hoffm., Pflanzenr. 147. XV (Heft 81): 45. 1922. TYPE: *Apodiscus chevalieri* Hutch.

A poorly understood monotypic genus from the Guinea region of west Africa; said by Pax and Hoffmann to be related to *Maesobotrya*.

46. Ashtonia Airy Shaw, Kew Bull. 357. 1968; Hook. Icon. Pl. 38: t. 3702. 1974; Whitmore, Tree Fl. Malaya 2: 62. 1972; Airy Shaw, Kew Bull. Add. Ser. 4: 42. 1975. TYPE: *Ashtonia excelsa* Airy Shaw.

An Old World genus of two species in Borneo and the Malay peninsula.

47. Aporusa Blume, Bijdr. 514. 1826 (as *Aporosa*); Fl. Jav. 1: viii. 1828; Muell. Arg., DC. Prodr. 15(2): 469. 1866; Bentham, Gen. Pl. 3: 282. 1880; Hook. f., Hook. Icon. Pl. 16: 5. 1583. 1887; Fl. Brit. Ind. 5: 345. 1887; Pax & Hoffm., Pflanzenr. 147. XV (Heft 81): 80. 1922; Backer & Bakh., Fl. Java 1: 455. 1963; Airy Shaw, Kew Bull. 30: 380. 1966; 23: 2. 1969; 25: 474. 1971; Thin, Công Trình Nghiên Cú'u Khoa Hoc 10: 82. 1986. TYPE: *Aporusa frutescens* Blume.

Leiocarpus Blume, Bijdr. 581. 1826. TYPE: *Leiocarpus fruticosus* Blume [= *Aporusa fruticosa* (Blume) Muell. Arg.; lectotype, designated by Wheeler, 1975].

Lepidostachys Wallich ex Lindley, Nat. Syst. ed. 2, 441. 1836. TYPE: *Lepidostachys roxburghii* Wallich ex Lindley [nom. illeg.; = *Aporusa dioica* (Roxb.) Muell. Arg.].

Scepa Lindley, Nat. Syst. ed. 2, 441. 1836. TYPE: *Scepa stipulacea* Lindley [= *Aporusa dioica* (Roxb.) Muell. Arg.].

A genus of 80 Old World species, from India and Sri Lanka to Indonesia and Melanesia (Solomon Islands).

Subtribe 6d. ANTIDESMINAE Muell. Arg., Linnaea 34: 64. 1865 (as Antidesmeae); Pax, Natürl. Pflanzenfam. ed. 1, 3(5): 26. 1890; Pax & Hoffm., Pflanzenr. 147. XV (Heft 81): 3. 1922. TYPE: *Antidesma* L.

Ordo Stilagineae C. A. Agardh, Aphor. Bot. 14: 199. 1824. TYPE: *Stilago* L. [= *Antidesma* L.].

Subtribe Hieronymeae Muell. Arg., Linnaea 34: 64. 1865. TYPE: *Hyeronima* Fr. Allem.

Dioecious (rarely monoecious) trees or shrubs (rarely herbs); leaves eglandular, stomata paracytic, stipules caducous; inflorescences axillary, ± amentlike; staminate bracts mostly 1-flowered; sepals 3–6, free or connate; petals mostly absent or reduced; disk lobed or dissected; stamens 3–6, free or nearly so, anthers with ± enlarged glandular connectives, anther-sacs usually pendulous; pollen grains prolate, 3-colporate, reticulate; pistillode present; carpels 1–3(–5), ovules anatropous; styles bifid (rarely entire); fruit capsular or drupaceous; seeds mostly 1 per locule or fruit; seed-coat dry; endosperm thin to copious, cotyledons broader than but scarcely exceeding radicle.

Subtribe Antidesminae corresponds to the family Stilaginaceae as recognized by Airy Shaw (1965, and many subsequent publications). However, pollen and foliar anatomical evidence clearly supports membership of *Antidesma* in the Euphorbiaceae. Two of the six genera (*Phyllanoa* and *Leptonema*) are not well understood, and their inclusion here must be regarded as provisional.

KEY TO THE GENERA OF SUBTRIBE ANTIDESMINAE

1a. Indumentum absent or of simple or stellate hairs.
  2a. Carpels 3–5; fruit dehiscent.
    3a. Disk present; ovary 3-locular.
      4a. Pistillode present; pistillate sepals not accrescent in fruit; pistillate flower sometimes with petals and staminodes.
        5a. Leaves entire; pistillate flowers not bracteolate; fruits pedicellate ____ 48. *Thecacoris*
        5b. Leaves dentate; pistillate flowers bracteolate; fruits subsessile ____ 49. *Phyllanoa*
      4b. Pistillode absent; pistillate sepals accrescent; pistillate flowers lacking petals or staminodes ____ 50. *Celianella*
    3b. Disk absent; ovary 4–5-locular ____ 51. *Leptonema*
  2b. Carpel solitary; fruit indehiscent ____ 52. *Antidesma*
1b. Indumentum lepidote; fruit indehiscent ____ 53. *Hyeronima*

48. Thecacoris A. Jussieu, Euphorb. Tent. 12. 1824; Baillon, Etude Gén. Euphorb. 605. 1858; Bentham, Gen. Pl. 3: 286. 1880; Pax & Hoffm., Pflanzenr. 147. XV (Heft 81): 8. 1922; Keay, Fl. W. Trop. Afr. ed. 2, 1: 371. 1958; Leandri, Fl. Madag. 1: 4. 1958; Radcliffe-Smith, Fl. Trop. E. Afr. Euphorb. 107. 1987. TYPE: *Thecacoris madagascariensis* A. Juss.

Cometia Du Petit Thouars ex Baillon, Etude, Gén. Euphorb. 642. 1858. TYPE: *Cometia thouarsii* Baillon [= *Thecacoris cometia* Leandri].

Cyathogyne Muell. Arg., Flora 47: 536. 1864. TYPE: *Cyathogyne viridis* Muell. Arg. [= *Thecacoris viridis* (Muell. Arg.) Leandri].

Baccaureopsis Pax, Bot. Jahrb. 43: 319. 1909. TYPE: *Baccaureopsis lucida* Pax [= *Thecacoris ludica* (Pax) Hutch.].

As here delimited, *Thecacoris* includes about 20 species from Africa and Madagascar. The herbaceous species have been segregated as a separate genus *Cyathogyne* by Mueller (1866) and Pax & Hoffmann (1922, 1931), but as noted by Radcliffe-Smith (1987), *Thecacoris usambarensis* Verdc. bridges the gap between the two generic concepts.

49. Phyllanoa Croizat, Caldasia 2: 123. 1943. TYPE: *Phyllanoa colombiana* Croizat.

A monotypic genus from the Colombian Andes, known only from the imperfect type specimen. The floral details of the pistillate flower, especially the staminodes, suggest a possible affinity with *Thecacoris*, although there is also a general resemblance to *Richeria*, in subtribe Scepinae.

50. Celianella Jablonski, Mem. New York Bot. Gard. 12: 176. 1965. TYPE: *Celianella montana* Jabl.

A monotypic genus of the Venezuelan Guayana highlands. The plant is distinctive in the semisucculent leaves and accrescent pistillate sepals. Levin (1986c) allied it with *Hyeronima* on the basis of foliar characters.

51. Leptonema A. Jussieu, Euphorb. Tent. 19. 1824; Bentham, Gen. Pl. 3: 275. 1880; Pax & Hoffm., Natürl. Pflanzenfam. ed. 2, 19c: 59. 1931; Leandri, Notul. Syst. (Paris) 6: 22. 1937; Mém. Inst. Sci. Madag. 8B: 212. 1957; Fl. Madag. 111(1): 12. 1958. TYPE: *Leptonema venosum* (Poir.) A. Juss.

A poorly known genus of two species endemic to Madagascar.

52. Antidesma Burman ex L., Sp. Pl. 1027. 1753; Gen. Pl. 451. 1754; Muell. Arg., DC. Prodr. 15(2): 247. 1866; Bentham, Gen. Pl. 3: 284. 1880; Hooker, Fl. Brit. Ind. 5: 354. 1887; Pax & Hoffm., Pflanzenr. 147. XV (Heft 81): 107. 1922; Airy Shaw, Kew Bull. 23: 277. 1969; 26: 457. 1972; 28: 269. 1973; 33: 15, 423. 1979; 36: 358, 635. 1981; Léonard, Bull. Jard. Bot. Nat. Belg. 58: 4. 1988. *Bestram* Adanson, Fam. Pl. 354. 1763. TYPE: *Antidesma alexiteria* L.

Stilago L., Mant. Pl. 16. 1767. TYPE: *Stilago bunius* L. [= *Antidesma bunius* (L.) Spreng.].

Rhytis Lour., Fl. Cochinchin. 660. 1790. TYPE: *Rhytis fruticosa* Lour. [= *Antidesma fruticosum* (Lour.) Muell. Arg.].

A large Old World genus of ca. 200 species, only 10 of which occur in Africa and Madagascar. The remainder of the species are Asian except for a few species in Australia and the Pacific islands.

53. Hyeronima Allemão, Pl. Novas Bras. 1. 1848; Muell. Arg., DC. Prodr. 15(2): 268. 1866 (as *Hieronyma*); Bentham, Gen. Pl. 3: 284. 1880; Pax & Hoffm., Pflanzenr. 147. XV (Heft 81): 31. 1922; Jablonski, Mem. New York Bot. Gard. 17: 122. 1967; Webster, Ann. Missouri Bot. Gard. 75: 1094. 1988; Franco, Bot. Jahrb. Syst. 111: 297. 1990. TYPE: *Hyeronima alchorneoides* Allemão.

Stilaginella Tul., Ann. Sci. Nat. III. 15: 240. 1851. TYPE: *Stilaginella laxiflora* Tul. [= *Hyeronima laxiflora* (Tul.) Muell. Arg.].

A neotropical genus of more than 20 described species, many of these difficult to distinguish. Franco (1990) recognized 10 species for South America, and there are a few additional species in the West Indies.

Subtribe 6e. PORANTHERINAE (Muell. Arg.) Köhler, Grana Palynologica 6: 99. 1965. Tribe Poranthereae Muell. Arg., Bot. Zeitung 22: 324. 1864. TYPE: *Poranthera* Rudge.

Monoecious or dioecious herbs or subshrubs; leaves ± ericoid; flowers in terminal corymbose racemes; sepals 5; petals present or absent; stamens 5; disk present; anthers pendulous; pistillode small or absent; pistillate disk annular; ovary 3-locular; ovules anatropous; styles bifid; fruits capsular; seeds 2 per locule; endosperm copious; cotyledons about as broad as radicle.

Two closely related Australasian genera. Their systematic position remains controversial. Pax & Hoffmann (1931) followed Mueller (1866) in placing tribe Porantheae in the division "Stenolobae," because of the narrow cotyledons. In 1975, I associated *Poranthera* with *Andrachne*, partly because of the pollen data of Punt (1962). However, Köhler (1965) showed that the pollen of *Poranthera* was more compatible with an affinity to the *Antidesma* complex, and he demoted Porantheae to a subtribe of Antidesminae. Because he did not cite the basionym, his combination was not validly published, and it presumably is validated here.

KEY TO THE GENERA OF SUBTRIBE PORANTHERINAE

1a. Monoecious; petals and pistillode present ..... 54. *Poranthera*

1b. Dioecious; petals and pistillode absent ..... 55. *Oreoporanthera*

54. Poranthera Rudge, Trans. Linn. Soc. London 10: 302. 1811; Bentham, Fl. Austral. 6: 54. 1873; Gen. Pl. 3: 262. 1880; Grüning, Pflanzenr. 147. (Heft 58): 13. 1913. TYPE: *Poranthera* Rudge.

Ten species from Australia.

55. Oreoporanthera Hutchinson, Amer. J. Bot. 56: 747. 1969. *Poranthera* sect. *Oreoporanthera* Grüning, Pflanzenr. 147. (Heft 58): 21. 1913. TYPE: *Oreoporanthera alpina* (Cheeseman) Hutchinson.

A monotypic genus endemic to New Zealand. As pointed out by Huft (pers. comm.) Hutchinson described *Oreoporanthera* as a new genus (with Latin description), even though he was obviously basing it on Grüning's section.

Tribe 7. HYMENOCARDIEAE (Muell. Arg.) Hutchinson, Amer. J. Bot. 56: 746. 1969. Phyllantheae subtribe Hymenocardieae Muell. Arg., Linnaea 34: 64. 1865. Hymenocardiaceae Airy Shaw, Kew Bull. 18: 261. 1965; Léonard & Mosango, Fl. Afr. Centrale, Hymenocardiaceae 1. 1985. TYPE: *Hymenocardia* Wall. ex Lindley.

Dioecious trees or shrubs; indumentum of simple hairs and sessile glands; leaves alternate, entire, penninerved, stipulate; inflorescences axillary, spicate, racemose, or paniculate; staminate sepals 4–8, connate; petals absent; stamens 4–8, filaments free or basally connate; anthers longitudinally dehiscent; pollen porate; pistillode present; pistillate flowers pedicellate; sepals 4 9, free, caducous; ovary 2-locular; styles 2, elongated, entire or lacerate, free; ovules anatropous, 2 per locule; fruit capsular or winged, samaroid; seeds 1 per locule; endosperm scanty; cotyledons broader and longer than radicle.

A distinctive group originally including a single Old World genus, considered to be a distinct family by a number of modern workers (e.g., Léonard & Mosango, 1985; Meeuse, 1990). However, most floral and anatomical details (e.g., in Levin, 1986a, b, c) indicate that it is better retained within the Euphorbiaceae. A second genus, *Didymocistus*, is provisionally included here, although it is very distinct from *Hymenocardia* in many ways, and could perhaps be placed in a separate tribe or subtribe.

KEY TO THE GENERA OF TRIBE HYMENOCARDIEAE

1a. Fruit capsular; inflorescence paniculate; styles lacerate ..... 56. *Didymocistus*

1b. Fruit samaroid; inflorescence racemose; styles papillose ..... 57. *Hymenocardia*

56. Didymocistus Kuhlmann, An. Prim. Reun. Sud-Amer. Bot. 3: 82. 1940. TYPE: *Didymocistus chrysadenius* Kuhlm.

A monotypic genus of Amazonian Brazil. Kuhlmann related it to *Aporusa*, but the anatomical studies of Levin (1986a, b, c) suggest that it is possibly closer to *Hymenocardia*. It does appear that *Didymocistus* may possibly represent a link between tribes Antidesmeae and Hymenocardieae.

57. Hymenocardia Wallich ex Lindley, Nat. Syst. ed. 2, 441. 1836; Muell. Arg., DC. Prodr. 15(2): 476. 1866; Oliver, Hook. Ic. Pl. 12: 29, t. 1131. 1873; Bentham, Gen.

Pl. 3: 284. 1880; Pax & Hoffm., Pflanzenr. 147. XV (Heft 81): 72. 1922; Léonard & Mosango, Fl. Afr. Centrale, Hymenocardiaceae 2. 1985; Radcliffe-Smith, Fl. E. Trop. Afr., Euphorbiaceae 577. 1988. TYPE: *Hymenocardia punctata* Wallich ex Lindl.

Samaropyxis Miquel, Fl. Ned. Ind., Erste Bijv. 464. 1861. TYPE: *Samaropyxis elliptica* Miq. [= *Hymenocardia wallichii* Tul.].

An Old World genus of eight species, of which seven are African and one southeast Asian; absent from Madagascar.

Tribe 8. BISCHOFIEAE (Muell. Arg.) Hurusawa, J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 6: 339. 1954. Phyllantheae subtribe Bischoffieae Muell. Arg., Linnaea 34: 64. 1865. Family Bischofiaceae (Muell. Arg.) Airy Shaw, Kew Bull. 18: 252. 1965. TYPE: *Bischofia* Blume.

A monotypic tribe of a single Asian species, very distinct from other Phyllanthoideae by virtue of its trifoliolate leaves. Although Airy Shaw (1965) suggested a relationship with the Staphyleaceae, evidence from embryology (Bhatnagar & Kapil, 1974) and leaf anatomy (Levin, 1986a, b, c) supports retention in the Euphorbiaceae.

58. Bischofia Blume, Bijdr. 1168. 1826; Muell. Arg., DC. Prodr. 15(2): 478. 1866; Bentham, Gen. Pl. 3: 280. 1880; Pax & Hoffm., Pflanzenr. 147. XV (Heft 81): 312. 1922; Airy Shaw, Kew Bull. 18: 253. 1965; 21: 327. 1967; A. C. Smith, Fl. Vitiensis Nova 2: 494. 1981. TYPE: *Bischofia javanica* Blume.

Microelus Wight & Arnott, Edinb. New Philos. J. 14: 298. 1833. TYPE: *Microelus roeperianus* Wight & Arnott [= *Bischofia javanica* Blume].

Stylodiscus Bennett, Pl. Jav. Rar. 133. 1840. TYPE: *Stylodiscus trifoliatus* (Roxb.) Bennett [*Andrachne trifoliata* Roxb. = *Bischofia javanica* Blume].

A genus of a single species distributed from India and Sri Lanka to China, Indonesia, and the Pacific islands.

INCERTAE SEDIS

59. Centroplacus Pierre, Bull. Mens. Soc. Linn. Paris II. 1: 114. 1899; Gilg, Bot. Jahrb. 40: 516. 1908; Hutchinson, Fl. Trop. Afr. 6(1): 629. 1912; Pax & Hoffm., Natürl. Pflanzenfam. ed. 2, 19c: 46. 1931. TYPE: *Centroplacus glaucinus* Pierre.

This genus is based on a single poorly known species from Gabon that was referred to a flacourtiaceous affinity by Pierre, but to the Euphorbiaceae by Gilg (1908) and Hutchinson (1912). Pax & Hoffmann (1931) placed it in the Antidesminae next to *Spondianthus*, but its place within the Euphorbiaceae still appears uncertain.

60. Meborea Aublet, Hist. Pl. Guiane 825. 1775; Lanjouw, Euphorb. Suriname 9, t. 1. 1931. TYPE: *Meborea guianensis* Aublet.

This monotypic genus from French Guiana was referred by Mueller (1866) to *Phyllanthus*. Lanjouw was unable to place the genus, but regarded it as not synonymous with *Phyllanthus*, a view with which I agree. Judging from Aublet's description and illustration, it seems probable that *Meborea* belongs to tribe Phyllantheae, but it cannot be identified with certainty.

Subfamily II. OLDFIELDIOIDEAE Köhler & Webster, J. Arnold Arbor. 48: 308. 1967; Webster, Taxon 24: 595. 1975. TYPE: *Oldfieldia* Benth.

Paivaeusaceae Meeuse, Euphorbiaceae Auct. Plur. 30. 1990. TYPE: *Paivaeusa* Welw. ex Benth. [= *Oldfieldia* Benth. & Hook.].

Monoecious or dioecious trees, shrubs, or subshrubs; leaves alternate or more commonly opposite or verticellate, simple or palmately compound, entire or dentate; stipules small and caducous or absent; inflorescences axillary, glomerulate, racemose, capitulate, or paniculate; flowers apetalous (except in *Croizatia*); staminate sepals (3-)4-8(-12), imbricate, usually free; disk intrastaminal or absent (extrastaminal in *Croizatia*); stamens (2)3-30, filaments free or connate; pollen grains spheroidal, tectate, exine mostly with conspicuous spines, brevicolporate or porate; pistillode present or absent; pistillate sepals (3-)4 8(-13), free; disk annular to lobed or dissected, or absent; ovary 2-4(-5)-locular; ovules 2 per locule (except in *Scagea*); styles entire or stigmatoid (rarely bifid); fruit capsular (rarely drupaceous); seeds 1 or 2 per locule, often carunculate, testa usually smooth and shiny; endosperm usually copious (rarely obsolete).

This most recently recognized subfamily includes 28 genera with only ca. 100 species, overwhelmingly found in the Southern Hemisphere.

KEY TO THE TRIBES OF SUBFAMILY OLDFIELDIOIDEAE

1a. Petals present; staminate disk extrastaminal, annular; styles twice bifid; ovules hemitropous ..... 9. CROIZATIEAE

1b. Petals absent; staminate disk dissected, intrastaminal or absent; styles entire or rarely once bifid; ovules anatropous.
2a. Pollen apertures four; vessel elements at least in part with scalariform perforation plates (except in *Tetracoccus*); staminate disk extrastaminal or absent; leaves simple ..... 10. PODOCALYCEAE
2b. Pollen with more than 4 apertures (rarely inaperturate); vessel elements with simple perforation plates; staminate disk intrastaminal or absent; leaves simple, unifoliolate, or palmately compound.
3a. Leaves simple; monoecious or dioecious trees, shrubs, or herbs; seeds mostly carunculate ..... 11. CALETIEAE
3b. Leaves compound, or if simple then lamina stipellate or stipules adnate to petiole; dioecious trees or shrubs; seeds carunculate or ecarunculate ..... 12. PICRODENDREAE

Tribe 9. **CROIZATIEAE** Webster, trib. nov.

TYPE: *Croizatia* Steyermark.

Folia alterna integra; discus annularis; petalae 5, imbricatae; stamina 5, antheris extrorsis; pollinis grana 3-colporata spinulosa; ovarium 3-loculare, stylis bis bifidis, ovulis hemitropis; semina ecarunculata, exalbuminata.

Dioecious trees or shrubs; leaves alternate, entire; stipules deciduous or persistent; flowers in axillary clusters; staminate sepals and petals 5, imbricate; disk annular; stamens 5, free, anthers introrse; pollen grains globose, 3-colporate, exinous spines conspicuous; pistillode present; pistillate sepals and petals 5, imbricate; disk annular, glabrous; ovary pubescent, 3-locular; styles free, twice bifid; ovules hemitropous; fruit capsular; columella persistent, dilated; seeds 1–2 per locule, ecarunculate; endosperm absent; cotyledons broader than and about equaling radicle.

The tribe is represented by the single genus *Croizatia*. This taxon shows clear affinities with the tribe Amanoeae in subfamily Phyllanthoideae, and it is more or less arbitrary where it is placed.

61. **Croizatia** Steyermark, Fieldiana 28: 308, fig. 57. 1952; Webster, Gillespie & Steyermark, Syst. Bot. 12: 6. 1987. TYPE: *Croizatia neotropica* Steyermark.

A neotropical genus of four species, distributed from Panama to Venezuela and Ecuador.

Tribe 10. **PODOCALYCEAE** Webster, trib. nov. TYPE: *Podocalyx* Klotzsch.

Folia alterna vel opposita, integra vel serrata; stipulae deciduae; discus ♂ nullus; petalae nullae; stamina 5–13, antheris extrorsis vel introrsis; pollinis grana 4-brevicolporata, echinata; ovarium 3-loculare, stylis integris, ovulis anatropis; semina albuminata.

Dioecious trees; leaves alternate or opposite, entire or serrate; stipules caducous. Inflorescences in thyrses or ebracteate cymes. Flowers apetalous, disk absent; staminate sepals (3)4 or 5, free or connate, imbricate; stamens 5–13, free; anthers extrorse or introrse; pollen grains 4-brevicolporate, echinate, tectum smooth; pistillode present or absent; pistillate sepals 4 or 5, imbricate, persistent; disk present or absent; ovary 3-locular; styles dilated, stigmatiform; ovules anatropous. Fruit capsular or drupaceous; seeds carunculate or ecarunculate; endosperm present; cotyledons plane or plicate, much broader than radicle.

This tribe includes three American genera that are different in many respects and are classified together on the basis of pollen characters (pollen grains with four shortened colpi). The differences between the genera are so striking that it seems necessary to assign them to different subtribes.

Key to the Subtribes of Tribe Podocalyceae

1a. Peduncle free from petiole; fruit capsular.
2a. Staminate sepals connate; pistillode present; staminate and pistillate flowers in elongated spikes; seeds ecarunculate; leaves alternate, entire ..... 10a. Podocalycinae
2b. Staminate sepals discrete; pistillode absent; pistillate flowers solitary or clustered; seeds carunculate; leaves alternate, opposite, or whorled, entire or dentate ..... 10b. Tetracoccinae
1b. Peduncle adnate to the petiole; staminate sepals discrete; pistillode absent; fruit drupaceous ..... 10c. Paradrypetinae

Subtribe 10a. **PODOCALYCINAE** Webster, subtr. nov. TYPE: *Podocalyx* Kl.

Folia alterna, integra; flores spicatis; antheris extrorsis; flos ♂ pistillodio; discus ♀ sericeus; fructus capsularis; cotyledones planis.

Trees with alternate leaves; stipules caducous; flowers in axillary spikes; staminate sepals 5, connate below; disk obsolete; stamens 5 or 6, anthers extrorse; pollen grains 4-colporate, echinate; pistillode present; pistillate flowers pedicellate; sepals 5, imbricate, persistent; disk cupular, sericeous; ovary sericeous; fruit capsular; columella slender, persistent; cotyledons plane.

This subtribe includes only the single genus *Podocalyx*.

62. **Podocalyx** Klotzsch, Arch. Naturgesch. 7: 202. 1841. *Richeria* sect. *Podocalyx* (Kl.)

Muell. Arg., DC. Prodr. 15(2): 469. 1866. TYPE: *Podocalyx loranthoides* Kl.

A monotypic genus restricted to Amazonian South America. Although Pax & Hoffmann (1922, 1931) and recent workers (e.g., Jablonski, 1967) have followed Mueller in treating *Podocalyx* as a section of *Richeria*, its pollen is completely different and characteristic of the subfamily Oldfieldioideae.

Subtribe 10b. TETRACOCCINAE G. Levin, subtr. nov. TYPE: *Tetracoccus* Engelm. ex Parry.

Frutices dioicae; folia simplicia, alterna, opposita, vel verticillata, dentata vel integra; stipulae 0; discus ♂ intrastaminalis, lobatus; stamina 4–10, antheris extrorsis; pollinis grana 4-porata, echinata; pistillodio 0; discus ♀ glabrus, lobatus; styli elongati; fructus capsularis; semina carunculata, albuminata, cotyledonibus plicatis.

Shrubs; leaves alternate, opposite, or whorled, margins toothed or entire; stipules absent; staminate flowers in axillary racemes or panicles, or fasciculate; pistillate flowers solitary or fasciculate, axillary; staminate sepals 4–10, discrete; disk intrastaminal, lobed; stamens 4–10, anthers extrorse; pollen grains 4-porate, tectum verruculose between spines; pistillode absent; pistillate sepals 5–13; disk lobed; ovary (2–)3–4(–5)-locular; styles elongated; fruit capsular; seeds carunculate; endosperm abundant; cotyledons plicate.

This monogeneric subtribe is very difficult to place and perhaps should constitute a distinct tribe. Vegetatively, *Tetracoccus* is intermediate between *Podocalyx* and *Paradrypetes* in phyllotaxy and leaf margins. In some characters, such as the intrastaminal staminate disk and verruculose pollen sexine, there is a closer resemblance between *Tetracoccus* and other tribes of Oldfieldioideae. Levin & Simpson (1994) would refer the Tetracoccinae to the tribe Picrodendreae.

63. Tetracoccus Engelmann ex Parry, W. Amer. Scientist 1: 13. 1885; Croizat, Bull. Torrey Bot. Club 69: 456. 1942; Dressler, Rhodora 56: 49. 1954. TYPE: *Tetracoccus dioicus* Parry.

Halliophytum I. M. Johnston, Contr. Gray Herb. 68: 88. 1923. TYPE: *Halliophytum fasciculatum* (S. Wats.) I. M. Johnston [= *Tetracoccus fasciculatus* (S. Wats.) Croizat; lectotype].

As interpreted by Dressler (1954), a genus of four species endemic to southwestern North America (southern California and adjacent Arizona, southern Baja California, and northern Mexico).

Subtribe 10c. PARADRYPETINAE G. Levin, Syst. Bot. 17: 78. 1992. TYPE: *Paradrypetes* Kuhlmann.

Leaves opposite, margin ± spinose; stipules enclosing apical bud; staminate flowers in ebracteate cymes, pistillate solitary, the penduncle in both sexes adnate to the subtending petiole; staminate sepals 3 or 4, free; disk obsolete; stamens 9–13, anthers extrorse; pistillode absent; pistillate sepals 4; ovary 3-locular; fruit drupaceous, 1-seeded; embryo with plicate cotyledons.

A monogeneric subtribe, considered by Levin to be closest to subtribe Podocalycinae.

64. Paradrypetes Kuhlmann, Arq. Inst. Biol. Veg. Rio Jan. 2: 84. 1935; Levin, Syst. Bot. 17: 74. 1992. TYPE: *Paradrypetes ilicifolia* Kuhlmann.

A genus of two South American species, one in the Amazonian rainforests, the other in the Brazilian Atlantic rainforest.

Tribe 11. CALETIEAE Muell. Arg., Bot. Zeit. 22: 34. 1865; DC. Prodr. 15(2): 190. 1866; Grüning, Pflanzenr. 147 (Heft 58): 21. 1913. TYPE: *Caletia* Baillon [= *Micrantheum* Desf.].

Dioecious or monoecious trees or shrubs; leaves alternate, opposite, or verticellate, simple, entire or dentate, stipules obscure or absent; flowers apetalous, in axillary clusters or panicles; staminal sepals 4–8(–12), free; disk present or absent; stamens 4–30, filaments usually free; anthers extrorse or latrorse; pollen grains spheroidal, with exinous spines, colporate or zonoporate; pistillode present or absent; pistillate sepals 3–8(–13), free; disk present or absent; ovary 2–5-locular; styles unlobed, ± elongated, often dilated; fruit capsular; seeds usually 1 per coccus, carunculate or ecarunculate; endosperm usually copious; cotyledons much broader or scarcely broader than the radicle.

This variable tribe of 4 subtribes with 15 genera is entirely paleotropical, and indeed except for *Hyaenanche*, the genera are nearly confined to Australasia (with a few species of *Austrobuxus* in Indonesia).

KEY TO THE SUBTRIBES OF TRIBE CALETIEAE

1a. Leaves whorled (at least in part); filaments shorter than anthers; pollen tectum granulose, exinous spines long _____ 11a. Hyaenanchinae
1b. Leaves alternate or opposite; filaments longer than anthers; pollen tectum smooth.
2a. Pollen grains zonoaperturate; stipules de-

ciduous or reduced; leaves opposite or if alternate then capsule fleshy.

3a. Leaves opposite; stamens free; anthers not apiculate; capsule dry; pistillate sepals persistent ..... 11b. Dissiliariinae

3b. Leaves alternate; stamens connate; anthers apiculate; capsule fleshy; pistillate sepals deciduous ..... 11c. Petalostigmatinae

2b. Pollen grains pantoporate; stipules deciduous or persistent; leaves alternate; capsule dry ..... 11d. Pseudanthinae

Subtribe 11a. HYAENANCHINAE Baillon ex Muell. Arg., Linnaea 34: 64. 1865 (as Hyaenancheae); DC. Prodr. 15(2): 479. 1866. Tribe Hyaenancheae (Baillon ex Muell. Arg.) Hutch., Amer. J. Bot. 56: 746. 1969. TYPE: *Hyaenanche* Lambert.

Toxicodendrinae Pax, Natürl. Pflanzenfam. ed. 1, 3(5): 31. 1890; Pax & Hoffm., Pflanzenr. 147. XV (Heft 81): 284. 1922. TYPE: *Toxicodendrum* Thunb. (non P. Miller) [= *Hyaenanche* Lambert].

Dioecious trees or shrubs; leaves opposite or verticillate, simple, coriaceous, stipules obscure or absent; flowers in axillary clusters or panicles; staminate sepals 4–8(–12), ± connate; disk absent; stamens 8–30, filaments free, much shorter than anthers; anthers introrse or extrorse; pollen grains 6- or 7-zonoporate, spinose, tectum granulose; pistillode absent; pistillate sepals 3–8, free, deciduous in fruit; disk absent; ovary 3–4-locular, sericeous; styles elongated, ± dilated; fruit capsular; seeds carunculate; endosperm sparse.

This subtribe is here circumscribed to include only the type genus *Hyaenanche*, as treated by Mueller and Pax & Hoffmann. Clearly *Hyaenanche* is a very isolated genus whose relationships are still uncertain. It is isolated in the tribe Caletieae because of the verruculose microsculpturing of the pollen sexine, which recalls genera of tribe Picrodendreae. There is some resemblance to the Sri Lankan genus *Mischodon* in habit and pollen morphology, but it still is not clear whether the two genera should be grouped together.

65. Hyaenanche Lambert, Descr. Cinchona 52, t. 10. 1797; Muell. Arg., DC. Prodr. 15(2): 479. 1866; Dyer, Gen. S. Afr. Fl. Pl. 1: 311. 1975. TYPE: *Hyaenanche globosa* (Gaertner) Lambert.

Toxicodendrum Thunberg, Kongl. Vetensk. Acad. Handl. 17: 188. 1796 (non *Toxicodendron* P. Miller, 1754); Bentham, Gen. Pl. 3: 280. 1880; Pax & Hoffm., Pflanzenr. 147. XV (Heft 81): 284. 1922. TYPE: *Toxicodendrum capense* Thunb. [= *Hyaenanche globosa* (Gaertner) Lambert].

A monotypic genus of the Cape region of South Africa. The seeds of *Hyaenanche* are unusual within the Oldfieldioideae in the scanty endosperm, green cotyledons, and production of a unique toxin (Hyaenanchin).

Subtribe 11b. DISSILARIINAE Pax & Hoffmann, Pflanzenr. 147. XV (Heft 81): 288. 1922. TYPE: *Dissiliaria* F. Muell.

Monoecious or dioecious trees or shrubs; leaves opposite, simple, entire; stipules reduced or absent; flowers in axillary panicles or clusters; staminate sepals 4–6, imbricate, free; disk absent; stamens 8–50, free; pollen grains with long to short spines, tectum smooth; pistillode absent; pistillate sepals 4–6, free; disk cupulate or absent; ovary 2- or 3-(rarely 4-)locular, glabrous; styles short; fruit capsular; seeds carunculate or ecarunculate.

This Australasian subtribe includes 6 genera with ca. 25 species. Generic limits require further critical study.

KEY TO THE GENERA OF SUBTRIBE DISSILARIINAE

1a. Pollen exine with elongated spines; pistillode mostly absent.
  2a. Dioecious; stamens 8–25; pistillate disk cupular or absent.
    3a. Seeds with fimbriate caruncle; ovary 3(–4)-locular; styles ovate, erect ..... 66. *Austrobuxus*
    3b. Seeds ecarunculate.
      4a. Styles elongated, recurved; ovary 3(–4)-locular ..... 67. *Dissiliaria*
      4b. Styles ovate, erect; ovary 2-locular ..... 68. *Canaca*
  2b. Monoecious; stamens ca. 50; pistillate disk of subulate segments ..... 69. *Whyanbeelia*
1b. Pollen exine with reduced spines; pistillode present.
  5a. Stamens 4–6; styles separated at base, recurved; seeds ecarunculate ..... 70. *Choriceras*
  5b. Stamens 8–17; styles proximate, not recurved; seeds carunculate ..... 71. *Longetia*

66. Austrobuxus Miquel, Fl. Ned. Ind. Suppl. 444. 1861; Steenis, Blumea 12: 362. 1964; Airy Shaw, Kew Bull. 25: 506. 1971; Kew Bull. 29: 303. 1974; Kew Bull. 35: 597. 1980; A. C. Smith, Fl. Vitiensis Nova 2: 495. 1981; McPherson & Tirel, Fl. Nouv.-Caléd. 14(1): 193. 1987. TYPE: *Austrobuxus nitidus* Miquel.

Bureavia Baillon, Adansonia 11: 83. 1873. TYPE: *Bureavia carunculata* (Baillon) Baillon [= *Austrobuxus carunculatus* (Baillon) Airy Shaw].

Choriophyllum Bentham, Hook. Icon. Pl. 13: 62, t.

1280. 1879. TYPE: *Choriophyllum malayanum* Bentham [= *Austrobuxus nitidus* Miq.].

In the circumscription of Airy Shaw (1974) and McPherson & Tirel (1987), *Austrobuxus* is the largest genus of subfamily Oldfieldioideae, with ca. 20 species. The distribution is disjunct, with areas in Malaya and western Indonesia, Queensland, New Caledonia, and Fiji, but absent from New Guinea.

67. Dissiliaria F. Mueller ex Baillon, Adansonia I. 7: 366. 1867; Bentham, Fl. Austral. 6: 90. 1873; Pax & Hoffm., Pflanzenr. 147. XV (Heft 81): 291. 1922; Airy Shaw, Muelleria 4: 220. 1980; Kew Bull. 35: 625. 1980. TYPE: *Dissiliaria baloghioides* F. Muell. ex Baillon [lectotype, selected here; the generic name was associated with that species in Baillon's original description].

According to Airy Shaw (1980), *Dissiliaria* includes three species endemic to Australia (Queensland).

68. Canaca Guillaumin, Arch. Bot. Caen 1: 74. 1927; Airy Shaw, Kew Bull. 25: 508. 1971. TYPE: *Canaca vieillardii* Guill.

As noted by Airy Shaw (1971), *Canaca* was originally misplaced in the Monimiaceae by Guillaumin but recognized as related to *Austrobuxus* by McKee. McPherson & Tirel (1987) followed Airy Shaw in relegating *Canaca* to synonymy of *Austrobuxus*. However, if *Dissiliaria* is maintained as distinct from *Austrobuxus*, it appears that *Canaca* is equally deserving of recognition. It is possible that all three genera should be combined under the name *Austrobuxus*.

69. Whyanbeelia Airy Shaw & Hyland, Kew Bull. 31: 375, fig. 2. 1976; Kew Bull. 35: 691. 1980. TYPE: *Whyanbeelia terra-reginae* Airy Shaw & Hyland.

A monotypic genus of tropical Australia (Queensland).

70. Choriceras Baillon, Adansonia I. 11: 119. 1873; Airy Shaw, Kew Bull. 14: 356. 1961; Muelleria 4: 220. 1980; Kew Bull. 35: 604. 1980. TYPE: *Choriceras australiana* Baillon [= *Choriceras tricorne* (Bentham) Airy Shaw].

A genus of two species restricted to tropical Australia and Papua. Although Pax & Hoffmann (1922) reduced *Choriceras* to a synonym of *Dissiliaria*, Airy Shaw (1961) pointed out its distinguishing characters.

71. Longetia Baillon ex Muell. Arg., DC. Prodr. 15(2): 244. Aug. 1866; Baillon, Adansonia I. 6: 352, t. 9. Oct. 1866; Bentham, Gen. Pl. 3: 279. 1880; Pax & Hoffm., Pflanzenr. 147. XV (Heft 81): 289. 1922; McPherson & Tirel, Fl. Nouv.-Caléd. 14(1): 188. 1987. TYPE: *Longetia buxoides* Baillon ex Muell. Arg.

As interpreted by McPherson & Tirel, *Longetia* is a monotypic genus endemic to New Caledonia. Pax & Hoffmann (1922) construed *Longetia* in a broad sense, including species now placed in *Austrobuxus*. Airy Shaw (1971, 1974) held a similar broad view, except that *Longetia* species were now transferred to *Austrobuxus*. In view of the distinct difference in pollen, McPherson's return to the classical concept of Baillon and Mueller seems fully justified.

Subtribe 11c. PETALOSTIGMATINAE Pax & Hoffmann, Pflanzenr. 147. XV (Heft 81): 281. 1922. Tribe Petalostigmateae (Pax & Hoffm.) Webster, Taxon 24: 595. 1975. TYPE: *Petalostigma* F. Muell.

Dioecious trees or shrubs; leaves alternate, simple, entire; stipules caducous; flowers in axillary clusters; staminate sepals 4–6, imbricate; disk absent; stamens 20–40, filaments connate below into a column; anther connective typically pilose; pollen grains with short spines; pistillode obscure or absent; pistillate sepals 4–8, imbricate; disk absent; ovary 3–4-locular, pubescent; styles dilated; fruit a fleshy capsule; seeds carunculate.

A monogeneric subtribe restricted to Australia and New Guinea (Papua).

72. Petalostigma F. Mueller, Hook. J. Bot. Kew Gard. Misc. 9: 16. 1857; Muell. Arg., DC. Prodr. 15(2): 273. 1866; Baillon, Adansonia I. 7: 352. 1867; Benth., Fl. Austral. 6: 92. 1873; Gen. Pl. 3: 277. 1880; Pax & Hoffm., Pflanzenr. 147. XV (Heft 81): 281. 1922; Airy Shaw, Kew Bull. 31: 366. 1976; Kew Bull. 35: 661. 1980. TYPE: *Petalostigma quadriloculare* F. Muell.

As treated by Airy Shaw (1980), *Petalostigma* is a genus of six variable Australian species, one of which extends to New Guinea (Papua).

Subtribe 11d. PSEUDANTHINAE Muell. Arg., Linnaea 34: 55. 1865; DC. Prodr. 15(2): 195. 1866. TYPE: *Pseudanthus* Sprengel.

Monoecious (rarely dioecious) trees, shrubs, or herbs; leaves mostly alternate, entire; stipules de-

ciduous or persistent; flowers in axillary clusters; staminate sepals 3–6, imbricate, free; disk intrastaminal or absent; stamens 3–20 (rarely more), filaments free or connate; pollen grains with long or short spines, tectum smooth; pistillode present or absent; pistillate sepals 4–6, free, usually persistent; disk present or absent; ovary 2–3-locular; styles unlobed, dilated or elongated; fruit capsular; seeds carunculate.

The subtribe Pseudanthinae is here circumscribed in concurrence with suggestions by Levin (pers. comm.) to include six Australasian genera. The referral of *Kairothamnus* and *Scagea* to the Pseudanthinae needs confirmation, but appears compatible with the anatomical and palynological evidence.

KEY TO THE GENERA OF SUBTRIBE PSEUDANTHINAE

1a. Cotyledons broader than radicle; trees or shrubs.
  2a. Staminate sepals 4; stamens 10–12 ..... 73. *Kairothamnus*
  2b. Staminate sepals (5)6; stamens 4–6.
    3a. Ovules 1 per locule; pistillode present; staminate inflorescence racemose or umbellate; stipules conspicuous but deciduous ..... 74. *Scagea*
    3b. Ovules 2 per locule; pistillode absent; staminate flowers in axillary glomerules; stipules minute or obsolete ..... 75. *Neoroepera*
1b. Cotyledons scarcely broader than radicle; herbs or undershrubs.
  4a. Stipules foliose; fruits 3-seeded; pollen grains with long exinous spines ..... 76. *Micrantheum*
  4b. Stipules not foliose; fruits 1-seeded; pollen grains with reduced spines.
    5a. Stamens free; pistillode present ..... 77. *Pseudanthus*
    5b. Stamens connate; pistillode absent ..... 78. *Stachystemon*

73. Kairothamnus Airy Shaw, Kew Bull. 34: 596. 1980; Kew Bull. Add. Ser. 8: 121, t. 1 fig. 1. 1980. TYPE: *Kairothamnus phyllanthoides* (Airy Shaw) Airy Shaw.

A monotypic genus of eastern New Guinea (Morobe District). The alternate caudate-acuminate leaves of this plant indeed give it an aspect suggestive of *Phyllanthus*, as noted by Airy Shaw, but its pollen is typical of the Oldfieldioideae, and the genus appears very close to *Austrobuxus*.

74. Scagea McPherson, Bull. Mus. Nat. Hist. Nat. Paris, IVB. 7: 247. 1985; Fl. Nouv.-Caléd. 14(1): 90. 1987. TYPE: *Scagea depauperata* (Baillon) McPherson.

A genus of two species endemic to New Caledonia. The genus was originally referred to subfamily Crotonoideae by McPherson because of the uniovulate carpels, but the pollen clearly suggests placement in the Oldfieldioideae. The genus appears very similar to *Choriceras*, but differs in ovule number and pollen morphology.

75. Neoroepera Muell. Arg. & F. Mueller, DC. Prodr. 15(2): 488. 1866; Bentham, Fl. Austral. 6: 116. 1873; Gen. Pl. 3: 276. 1880; Airy Shaw, Kew Bull. 35: 658. 1980. TYPE: *Neoroepera buxifolia* Muell. Arg. & F. Muell.

A genus to two species endemic to Australia (Queensland).

76. Micrantheum Desf., Mém. Mus. Hist. Nat. Paris 4: 253, t. 14. 1818; Muell. Arg., DC. Prodr. 15(2): 195. 1866; Bentham, Fl. Austral. 6: 58. 1873; Gen. Pl. 3: 262. 1880; Grüning, Pflanzenr. 147. (Heft 58): 23. 1913; Pax & Hoffm., Natürl. Pflanzenfam. ed. 2, 19c: 224. 1931. TYPE: *Micrantheum ericoides* Desf.

Caletia Baillon, Etude Gén. Euphorb. 553. 1858. TYPE: *Caletia micrantheoides* Baillon, nom. illeg. [= *Micrantheum hexandrum* Hook. f.].

Allenia Ewart, Proc. Roy. Soc. Vict. II. 22: 7. 1909. TYPE: *Allenia blackiana* Ewart, nom. illeg. [= *Micrantheum demissum* F. Muell.].

A genus of three Australian species.

77. Pseudanthus Sieber ex Sprengel, Syst. Veg. 4(2): 22, 25. 1827; Muell. Arg., DC. Prodr. 15(2): 196. 1866; Bentham, Fl. Austral. 6: 58. 1873; Gen. Pl. 3: 262. 1880; Grüning, Pflanzenr. 147. (Heft 58): 26. 1913. TYPE: *Pseudanthus pimeleoides* Sieber ex Sprengel.

Chrysostemon Klotzsch, Pl. Preiss. 2: 232. 1848. TYPE: *Chrysostemon virgatus* Kl. [= *Pseudanthus virgatus* (Kl.) Muell. Arg.].

Chorizotheca Muell. Arg., Linnaea 32: 76. 1863. TYPE: *Chorizotheca micrantheoides* Muell. Arg. [= *Pseudanthus virgatus* (Kl.) Muell. Arg.].

An Australian genus of seven or eight species.

78. Stachystemon Planchon, Hook. London J. Bot. 4: 471, t. 15. 1845; Muell. Arg., DC. Prodr. 15(2): 198. 1866; Bentham, Fl. Austral. 6: 61. 1873; Gen. Pl. 3: 263. 1880; Grüning, Pflanzenr. 147 (Heft 58): 32. 1913; Pax & Hoffm., Natürl. Pflanzenfam. ed. 2, 19c: 226. 1931. TYPE: *Stachystemon vermiculare* Planch.

A genus of three species in western Australia.

Tribe 12. PICRODENDREAE (Small) Webster, Taxon 24: 595. 1975. Family Picrodendraceae Small, J. New York Bot. Gard. 18: 184. 1917. TYPE: *Picrodendron* Planchon.

Monoecious or dioecious trees or shrubs; leaves alternate or opposite, 3–9-parted (rarely unifoliolate), entire; stipules caducous, fused to petiole, or absent; flowers in axillary cymes, racemes, or glomerules; staminate sepals 4–8 (or obsolete), free; disk intrastaminal or absent; stamens 4–50, free; anthers extrorse or introrse; pollen grains spheroidal, brevicolporate or porate, with exinous spines, tectum granulose; pistillode minute or absent; pistillate sepals 4–8, persistent or deciduous; disk present or absent; ovary 2–3-locular; styles elongated or stigmatiform; fruit capsular or drupaceous; seeds carunculate or ecarunculate; endosperm usually copious; cotyledons broader and longer than radicle.

This tribe of ten genera in three subtribes contrasts markedly with the Caletieae in its distribution: all the genera are either American or African/Madagascan, with one genus (*Mischodon*) in Sri Lanka. The tribe is generally well characterized by its compound leaves, although the leaf blade appears unifoliolate in *Mischodon*, some species of *Androstachys*, and *Parodiodendron*.

KEY TO THE SUBTRIBES OF TRIBE PICRODENDREAE

1a. Stipules caducous or obsolete, free from petiole.
  2a. Staminate sepals free; capsule septicidal ..... 12a. Picrodendrinae
  2b. Staminate sepals connate; capsule loculicidal ..... 12b. Paivaeusinae
1b. Stipules persistent, ± adnate to petiole; seeds ecarunculate ..... 12c. Mischodontinae

Subtribe 12a. PICRODENDRINAE (Small) Webster, stat. nov. Family Picrodendraceae Small, J. New York Bot. Gard. 18: 184. 1917. TYPE: *Picrodendron* Planchon.

Dioecious trees or shrubs; leaves alternate; leaves 3-foliolate or 1-foliolate, margins entire; stipules small and caducous or absent; inflorescences axillary, cymose, sometimes reduced to catkins or glomerules; staminate sepals 4–8, free or obsolete; disk intrastaminal or absent; stamens 5–15, free; pollen grains 5–8-porate or brevicolporate, sexine with long spines and verruculose tectum; pistillode minute or absent; pistillate sepals 4–8, deciduous; disk cupular or absent; ovary 2-or 3-locular; styles elongated or stigmatiform; fruit capsular or drupaceous; seeds 1 or 2 per locule, carunculate or ecarunculate.

The four American genera of tribe Picrodendreae are all referable to this subtribe.

KEY TO THE GENERA OF SUBTRIBE PICRODENDRINAE

1a. Leaves mostly 3–5-foliolate.
  2a. Fruits dehiscent; staminate sepals not reduced.
    3a. Stamens 6; pistillate flowers solitary ..... 79. *Celaenodendron*
    3b. Stamens 8–15; pistillate flowers racemose ..... 80. *Piranhea*
  2b. Fruits indehiscent, drupaceous; staminate sepals reduced ..... 81. *Picrodendron*
1b. Leaves simple (unifoliolate), stipellate; pistillate sepals foliose, persistent ..... 82. *Parodiodendron*

79. Celaenodendron Standley, Contr. Dudley Herb. 1: 76. 1927. TYPE: *Celaenodendron mexicanum* Standley.

A monotypic genus of western Mexico (Tres Marias Islands, Jalisco).

80. Piranhea Baillon, Adansonia I. 6: 235. 1866; Muell. Arg., Fl. Brasil. 11(2): 79. 1873; Bentham, Gen. Pl. 3: 281. 1880; Pax & Hoffm., Pflanzenr. 147. XV (Heft 81): 295. 1922; Jablonski, Mem. New York Bot. Gard. 17: 121. 1967. TYPE: *Piranhea trifoliolata* Baillon.

A genus of two species endemic to South America.

81. Picrodendron Planchon, Hook. London J. Bot. 5: 579. 1846; nom. cons. prop.; Krug & Urban, Bot. Jahrb. 15: 308. 1893; Fawc. & Rend., J. Bot. 55: 268. 1917; Hayden et al., J. Arnold Arbor. 65: 110. 1984. TYPE (typ. cons.): *Picrodendron baccatum* (L.) Krug & Urban.

A monotypic genus endemic to the West Indies (Greater Antilles, Bahamas, Cayman Islands, Swan Islands).

82. Parodiodendron Hunziker, Kurtziana 5: 331, fig. 1. 1969. TYPE: *Parodiodendron marginivillosum* (Speg.) Hunziker.

A monotypic genus of northern Argentina.

Subtribe 12b. PAIVAEUSINAE Pax & Hoffmann, Pflanzenr. 147. XV (Heft 81): 294. 1922. TYPE: *Paivaeusa* Welw. ex Bentham [= *Oldfieldia* Benth. & Hook. f.].

Dioecious trees; leaves alternate or opposite, 5–8-foliolate; stipules obsolete; staminate inflorescences in pedunculate ± congested cymes, the pistillate usually reduced to 1–3 flowers; staminate sepals 5–8, basally connate; disk intrastaminal, lobed; stamens

4–12, free, anthers extrorse; pistillode minute or absent; pistillate sepals 5–8, persistent; disk annular; ovary 2–3-locular; styles dilated, lobed; capsule tardily loculicidally dehiscent; seeds carunculate.

As circumscribed here, in agreement with the studies of Levin, subtribe Paivaeusinae includes only the single African genus *Oldfieldia*. Pax & Hoffmann (1922) also included in the Paivaeusinae *Piranhea*, which is here referred to Picrodendrinae, and *Aristogeitonia*, which appears better placed in Mischodontinae.

83. Oldfieldia Bentham & Hooker f., Hook. J. Bot. Kew Gard. Misc. 2: 184. 1850; Bentham, Gen. Pl. 3: 281. 1880; Pax & Hoffm., Pflanzenr. 147. XV (Heft 81): 297. 1922; Milne-Redhead, Kew Bull. 1948: 456. 1948; Léonard, Bull. Jard. Bot. Brux. 26: 338. 1956; Radcliffe-Smith, Fl. Trop. E. Afr., Euphorb. 114. 1987. TYPE: *Oldfieldia africana* Benth. & Hook.

Paivaeusa Welw. ex Benth., Gen. Pl. 1: 993. 1867. TYPE: *Paivaeusa dactylophylla* Welw. ex Oliver [= *Oldfieldia dactylophylla* (Welw. ex Oliver) Léonard].

Cecchia Chiovenda, Fl. Somala 2: 397, fig. 227. 1932. TYPE: *Cecchia somalensis* Chiovenda [= *Oldfieldia somalensis* (Chiovenda) Milne-Redhead].

As delimited by Léonard (1956) and Radcliffe-Smith (1987), *Oldfieldia* includes four African species. The distinction in phyllotaxy (alternate vs. opposite leaves) used by Pax & Hoffmann to distinguish *Paivaeusa* is clearly unworkable, because alternate and opposite leaves occur in both *Paivaeusa* and *Oldfieldia*.

Subtribe 12c. MISCHODONTINAE Muell. Arg., Linnaea 34: 202. 1865; DC. Prodr. 15(2): 1124. 1866; Webster, Taxon 24: 595. 1975. TYPE: *Mischodon* Thwaites.

Androstachydaceae Airy Shaw, Kew Bull. 18: 250. 1965. TYPE: *Androstachys* Prain.

Monoecious or dioecious trees or shrubs; leaves alternate or opposite, simple or 3-foliolate, entire; stipules persistent, adnate to petiole; flowers in axillary cymes or clusters; staminate sepals (2 -)5–8, free; disk intrastaminal or absent; stamens 5–50, free; pistillode present or absent; pistillate sepals 5 or 6, deciduous; disk annular or absent; ovary 3–4(–5)-locular, glabrous or pubescent; styles slightly to distinctly connate below; fruit capsular; seeds ecarunculate.

KEY TO THE GENERA OF SUBTRIBE MISCHODONTINAE

1a. Leaves alternate; pistillode present _____ 84. *Aristogeitonia*

1b. Leaves opposite; staminate disk or pistillode (or both) absent.

2a. Stamens with filaments elongated, free; leaves simple.

3a. Staminate disk absent; pistillode present; pistillate sepals deciduous __ 85. *Mischodon*

3b. Staminate disk present; pistillode absent; pistillate sepals accrescent in fruit _____ 86. *Voatomalo*

2b. Stamens with filaments united into a long column, anthers subsessile; leaves 1–7-foliolate.

4a. Leaves unifoliolate; fruit apically depressed _____ 87. *Androstachys*

4b. Leaves 3–7-foliolate; fruit beaked _____ 88. *Stachyandra*

84. Aristogeitonia Prain, Kew Bull. Misc. Inf. 1908: 439. 1908; Hook. Icon. Pl. 30: t. 2926. 1911; Fl. Trop. Afr. 6(1): 625. 1912; Pax & Hoffm., Pflanzenr. 147. XV (Heft 81): 296. 1922; Airy Shaw, Kew Bull. 26: 495. 1972; Radcliffe-Smith, Fl. E. Trop. Euphorb. 1: 118. 1987; Radcliffe-Smith, Kew Bull. 43: 627. 1988. TYPE: *Aristogeitonia limoniifolia* Prain.

Paragelonium Leandri, Bull. Soc. Bot. France 85: 231. 1939. TYPE: *Paragelonium perrieri* Leandri [= *Aristogeitonia perrieri* (Leandri) Radcl.-Sm.].

An African genus of three species (Angola, Kenya, Tanzania, and Madagascar). Radcliffe-Smith (1988) has recently demonstrated that *Paragelonium* from Madagascar cannot be separated from the mainland African *Aristogeitonia*.

85. Mischodon Thwaites, Hook. J. Bot. Kew Gard. Misc. 6: 299. 1854; Muell. Arg., DC. Prodr. 15(2): 1124. 1866; Bentham, Gen. Pl. 3: 280. 1880; Hook. f., Fl. Br. Ind. 5: 344. 1887; Pax & Hoffm., Pflanzenr. 147. XV (Heft 81): 292. 1922; Raju, J. Econ. Tax. Bot. 5: 165. 1984. TYPE: *Mischodon zeylanicus* Thwaites.

A monotypic genus of Sri Lanka; perhaps native (but very rare) in southern India.

86. Voatomalo Capuron ex Bosser, Adansonia II. 15: 333. 1976. TYPE: *Voatomalo eugenioidea* Capuron ex Bosser.

This genus of two species from Madagascar was mentioned by Leandri (1958) but not formally published until 1976.

87. Androstachys Prain, Kew Bull. Misc. Inf. 1908. 438. 1908; Fl. Trop. Afr. 6(1): 740. 1912; Pax & Hoffm., Pflanzenr. 147. XV (Heft 81): 287. 1922; Leandri, Fl. Madag. 111: 197. 1958; Airy Shaw, Kew Bull. 18: 251. 1965; Adansonia II. 10: 519. 1970; Dyer, Gen. S.

Afr. Fl. Pl. ed. 3, 312. 1975; Leroy, C. R. Acad. Sci. Paris 283D: 147. 1976; Alvin, Ann. Bot. 59: 579. 1987. TYPE: *Androstachys johnsonii* Prain [= *Androstachys subpeltata* (Sim) Phillips].

If *Stachyandra* is recognized as a distinct genus, *Androstachys* becomes a monotypic genus confined to eastern Africa.

88. Stachyandra Leroy ex Radcliffe-Smith, Kew Bull. 45: 562. 1990. TYPE: *Stachyandra merana* (Airy Shaw) Leroy ex Radcl.-Sm.

This genus of four Madagascan species has recently been segregated from *Androstachys*. The two taxa are closely related, and it might be more appropriate to treat *Stachyandra* as a subgenus of *Androstachys*.

Subfamily III. ACALYPHOIDEAE Ascherson, Fl. Prov. Brandenb. 1: 58. 1864. Family Acalyphaceae Klotzsch & Garcke, Monatsber. Königl. Preuss. Akad. Wiss. Berlin 1859: 246. 1859. TYPE: *Acalypha* L.

Trees, shrubs, or herbs; milky latex absent (rarely present, or represented by colored exudate); indumentum simple or hairs often branched or lepidote; leaves alternate (rarely opposite), usually stipulate; blade simple or palmately lobed (rarely compound), often with foliar glands. Inflorescences axillary or terminal, racemose or spicate, or reduced to glomerules or solitary flowers; bracts sometimes glandular. Staminate flower: sepals imbricate or often valvate (and then often connate and rupturing at anthesis); petals and disk present or absent; stamens 2–100+, free or connate; pollen grains mostly 3–4-colporate, exine semitectate (very rarely echinate); male gametophyte binucleate; pistillode present or absent. Pistillate flower: sepals (2–)3–6(–12), imbricate or open at anthesis, sometimes connate; petals and disk present or absent; ovary mostly 2–4-locular; styles entire to bifid or multifid; ovules solitary in each locule (except in *Dicoelia*), anatropous. Fruit capsular or rarely baccate or drupaceous; seeds carunculate or ecarunculate, testa sometimes fleshy; endosperm usually copious; cotyledons longer and broader than radicle. Base chromosome numbers mostly 9, 10, or 11.

With 116 genera in 20 tribes, subfamily Acalyphoideae is the largest and most complex of the subfamilies of Euphorbiaceae. Through *Clutia* it approaches the Phyllanthoideae, and through *Omphalea* both the Crotonoideae and Euphorbioideae. These multiple connections suggest that the Acalyphoideae may not be a monophyletic group.

KEY TO THE TRIBES OF SUBFAMILY ACALYPHOIDEAE

1a. Staminate flowers with 5 imbricate sepals and petals, 5 stamens, and perforate-tectate pollen grains; indumentum simple or malpighiaceous; dioecious; fruit capsular.
  2a. Petals not adaxially barbate; filaments connate; disk segments glandular-lobed; seeds carunculate; leaves usually pellucid-punctate, indumentum simple ____ 13. CLUTIEAE
  2b. Petals adaxially barbate; filaments free; disk segments not glandular-lobed; seeds ecarunculate; leaves not pellucid-punctate ____ 14. POGONOPHOREAE
1b. Staminate flowers not with 5 imbricate sepals and petals and 5 stamens (or if so, then pollen not perforate-tectate or fruit not capsular).
  3a. Staminate sepals distinctly imbricate, or else flowers enclosed in bibracteolate involucre; flowers apetalous; dioecious trees or shrubs.
    4a. Leaves alternate; pollen exine rugulose or micropunctate.
      5a. Filaments connate; pistillode conspicuous; pollen tectum not spinulose; seeds carunculate, testa dry.
        6a. Flowers in axillary glomerules, not involucrate; stamens 8–15; styles elongated, bifid; capsule echinate; leaves stipulate ____ 15. CHAETOCARPEAE
        6b. Flowers enclosed in bibracteolate involucres; stamens 2–6; styles abbreviated, dilated; capsule not echinate; leaves exstipulate ____ 16. PEREAE
      5b. Filaments free; pistillode small or absent; pollen tectum spinulose; seeds ecarunculate, testa fleshy ____ 17. CHEILOSEAE
    4b. Leaves opposite; pollen exine reticulate; seeds ecarunculate, testa dry ____ 18. ERISMANTHEAE
  3b. Staminate sepals valvate or slightly imbricate; flowers not in bibracteolate involucres; petals present or absent; pollen grains various, not micropunctate; indumentum various.
    7a. Staminate petals with depressions opposite anthers, or else fruit drupaceous with channeled endocarp.
      8a. Ovules 2 per locule; fruit capsular; plants monoecious; styles unlobed ____ 19. DICOELIEAE
      8b. Ovules 1 per locule; fruit drupaceous; plants dioecious; styles bifid ____ 20. GALEARIEAE
    7b. Staminate petals lacking depressions opposite anthers; fruit not drupaceous with channeled endocarp.
      9a. Cotyledons scarcely broader than radicle; monoecious (rarely dioecious) herbs or subshrubs with ericoid foliage; indumentum simple; pollen grains perforate-tectate, colpi distinctly marginate; seeds carunculate ____ 21. AMPEREAE
      9b. Cotyledons distinctly broader than radicle; habit otherwise.

10a. Petals present, at least in staminate flowers.
11a. Dioecious; indumentum simple; anther connective enlarged, anther sacs pendulous; pollen sexine coarsely reticulate, not heterobrochate ___ 22. AGROSTISTACHYEAE
11b. Monoecious (rarely dioecious); indumentum (at least in part) malpighiaceous, stellate, or lepidote; anthers not with enlarged connective and pendulous anther-sacs; pollen sexine often distinctly heterobrochate _____ 23. CHROZOPHOREAE
10b. Petals absent.
12a. Styles free or basally connate (if long-connate, then styles bifid or indumentum stellate); plants rarely scandent; stinging hairs absent.
13a. Staminate disk present; pollen exine coarsely reticulate, colpi mostly inoperculate.
14a. Leaves usually with laminar glands; indumentum simple or stellate; inflorescence axillary or terminal.
15a. Pollen colpi not marginate; staminate disk massive, pubescent; anther connective enlarged _____ 24. CARYODENDREAE
15b. Pollen colpi marginate; staminate disk tenuous, glabrous; anther connective not enlarged _____ 25. BERNARDIEAE
14b. Leaves eglandular; indumentum simple; stamens many; inflorescence axillary _____ 26. PYCNOCOMEAE
13b. Staminate disk absent (or if present, then pollen colpi operculate).
16a. Pollen grains coarsely reticulate or perforate-tectate; indumentum stellate; stamens inflexed in bud (except in *Koilodepas*); monoecious; pistillate calyx often accrescent; seeds ecarunculate _____ 27. EPIPRINEAE
16b. Pollen grains finely perforate-tectate to rugulose; indumentum simple or stellate; stamens not inflexed in bud.
17a. Pollen grains with operculate colpi; staminate disk present or absent; seeds mostly ecarunculate, testa not fleshy; stipules deciduous or obsolete.
18a. Leaves eglandular; styles subentire to multifid; staminate disk (if present) extrastaminal or interstaminal; pollen sexine finely perforate-tectate (nanospinules regularly arranged) _____ 28. ADELIEAE
18b. Leaves usually with embedded laminar glands; styles entire or if divided then inflorescences terminal; staminate disk (if present) intrastaminal; pollen sexine rugulose to striate (nanospinules not regularly arranged) _____ 29. ALCHORNEAE
17b. Pollen colpi inoperculate, often reduced; seeds carunculate or ecarunculate, testa dry or fleshy ____ 30. ACALYPHEAE
12b. Styles unlobed, mostly connate into a distinct column; often scandent or twining, sometimes with stinging hairs; inflorescences mostly terminal or pseudoaxillary, bisexual; seeds ecarunculate, testa dry.
19a. Staminate sepals valvate, splitting apart at anthesis; latex absent; inflorescence not paniculate; bracts eglandular; filaments free or connate _____ 31. PLUKENETIEAE
19b. Staminate sepals imbricate; latex clear or reddish; inflorescence paniculate; bracts foliose and biglandular; stamens 2 or 3, filaments connate; pollen grains colporate, exine rugulose _____ 32. OMPHALEAE

Tribe 13. CLUTIEAE (Muell. Arg.) Pax, Natürl. Pflanzenfam. ed. 1, 3(5): 81. 1890 (as Cluytieae). Hippomaneae subtribe Cluytieae Muell. Arg., Linnaea 34: 202. 1865. Cluytieae subtribe Cluytiinae Pax, Pflanzenr. 147. III (Heft 47): 49. 1911. TYPE: *Clutia* L.

Dioecious (rarely monoecious) perennial herbs or shrubs; indumentum simple or absent; leaves alternate, simple, entire, penninerved, often pellucid-punctate, eglandular; stipules small or obsolete; flowers in axillary glomerules (pistillate often solitary); sepals 5, imbricate; petals 5, free; disk dissected, segments 5, ± palmately lobed or glandular; stamens 5, filaments connate; anthers muticous, introrse; pollen grains prolate, 3-colporate, colpi inoperculate and slightly to distinctly marginate, exine perforate-tectate; pistillode present; ovary 3-(rarely 4-)locular, glabrous or pubescent; styles free or nearly so, bifid; fruit capsular; seeds carunculate, smooth (or rarely punctate), testa dry; endosperm copious; cotyledons broader and somewhat longer than the radicle.

As here interpreted, the tribe Clutieae is restricted

to the type genus *Clutia*, in accordance with the original concept of Mueller. None of the genera associated in subtribe Clutiinae by Pax (1911) are at all closely related to *Clutia*. Jussieu (1824) had placed *Clutia* in the tribe Phyllantheae, presumably because of its striking similarity in habit. Baillon (1858), who clearly demonstrated that *Clutia* has uniovulate carpels, considered the resemblance to *Briedelia* and *Phyllanthus* to be superficial, and suggested an affinity with *Chiropetalum*. However, the pollen structure does not support Baillon's view, and in fact is more compatible with Jussieu's original suggestion of a relationship with the Phyllanthoideae.

89. Clutia L., Sp. Pl. 1042. 1753; Gen. Pl. ed. 5, 464. 1754; Muell. Arg., DC. Prodr. 15(2): 1043. 1866; Bentham, Gen. Pl. 3; 302. 1880; Pax, Pflanzenr. 147. III (Heft 47): 50. 1911; Hutchinson, Fl. Trop. Afr. 6(1): 801. 1912; Prain, Fl. Cap. 5(2): 427. 1920; Dyer, Gen. S. Afr. Fl. Pl. 1: 321. 1975; Léonard, Fl. Congo Belge 8(1): 93. 1962; Radcliffe-Smith, Fl. E. Trop. Afr., Euphorb. 1: 331. 1987. TYPE: *Clutia pulchella* L.

A large African genus of ca. 75 species, with two extending to tropical Arabia; the greatest diversity is in South Africa.

14. Tribe POGONOPHOREAE (Muell. Arg.) Webster, Taxon 24: 595. 1975. Hippomaneae subtribe Pogonophoreae Muell. Arg., Linnaea 34: 202. 1865; DC. Prodr. 15(2): 1040. 1866. TYPE: *Pogonophora* Miers.

Dioecious trees; indumentum simple or (in inflorescence) malpighiaceous; leaves alternate, simple, entire, penninerved, eglandular; stipules very small or obsolete; inflorescences axillary, of thyrses or glomerules; staminate sepals 5, coriaceous, broadly imbricate (± biseriate); petals 5, imbricate, adaxially barbate; disk intrastaminal, urceolate, 5-lobed; stamens 5, filaments free; anthers basifixed, elongated; pollen grains prolate, 3-colporate, colpi inoperculate, not marginate, sexine perforate-tectate; pistillode present; pistillate perianth as in staminate; disk cupulate, tenuous; ovary 3-locular; styles bilobed; fruit capsular, seeds ecarunculate, smooth, shining, hilum large; endosperm copious; cotyledons much longer and broader than radicle.

The tribe Pogonophoreae is unigeneric, with the same circumscription as that of Mueller (1866). The relationships of the genus *Pogonophora* have remained problematical; affinities have been suggested with *Micrandra*, *Microdesmis*, and it has even been claimed that the membership of the taxon in the Euphorbiaceae is suspect. Airy Shaw (1966) suggested that it may be more closely allied to the Icacinaceae. However, the pollen of *Pogonophora* is similar to that of *Clutia*, and the floral resemblances to the Icacinaceae are probably superficial.

90. Pogonophora Miers ex Bentham, Hook. J. Bot. Kew Gard. Misc. 6: 372. 1854; Muell. Arg., DC. Prodr. 15(2): 1040. 1866; Fl. Bras. 11(2): 435. 1874; Bentham, Gen. Pl. 3: 288. 1880; Pax, Pflanzenr. 147. III (Heft 47): 108. 1911; Letouzey, Adansonia II. 9: 275. 1969; Secco, Rev. Gen. *Anomalocalyx* . . . Amer. Sul, 88. 1990. TYPE: *Pogonophora schomburgkiana* Miers ex Bentham.

A genus of two species, one neotropical (Amazonian and coastal Brazil), the other west African.

Tribe 15. CHAETOCARPEAE (Muell. Arg.) Webster, Taxon 24: 595. 1975. Hippomaneae subtribe Chaetocarpeae Muell. Arg., Linnaea 34: 202. 1865. TYPE: *Chaetocarpus* Thwaites.

Dioecious trees or shrubs; indumentum simple or absent; leaves alternate, simple, entire, penninerved, eglandular; stipules deciduous; flowers in axillary bracteate glomerules; staminate sepals 4 or 5, imbricate, free or connate; petals present or absent; disk dissected; stamens 5–15, filaments hirsute, connate below; anthers dehiscing longitudinally; pollen grains globose, 3-colporate (colpi with irregular margins), exine rugulose and micropunctate; pistillode prominent, hirsute; pistillate sepals 4–8, imbricate; disk urceolate; ovary 3-locular; styles bipartite, papillose; fruit capsular; seeds smooth, blackish, carunculate; endosperm copious; cotyledons broader and longer than radicle.

This taxon, originally including only the type genus, was enlarged by Webster (1975) through the inclusion of *Trigonopleura*. The close similarity of the pollen in the two genera seems decisive as an indication of affinity. The blackish carunculate seeds are reminiscent of those of *Clutia*. There may also be a more distant relationship with *Cheilosa*, as suggested by Pax & Hoffmann (1912). Airy Shaw (1975) independently suggested a tribe Chaetocarpeae (not formally published) including *Chaetocarpus* and *Trigonopleura*, and saw a resemblance to *Casearia* in the Flacourtiaceae.

KEY TO THE GENERA OF TRIBE CHAETOCARPEAE

1a. Petals present; anthers nearly sessile on staminal column; ovary smooth _____ 91. *Trigonopleura*

1b. Petals absent; filaments well developed; ovary echinate ____ 92. *Chaetocarpus*

91. Trigonopleura Hook. f., Fl. Brit. Ind. 5: 399. 1887; Hook. Icon. Pl. 18: t. 1753. 1888; Pax & Hoffm., Pflanzenr. 147. III (Heft 47: 95). 1911; Merrill, Phil. J. Sci. 11C: 76. 1916; Ridley, Fl. Malay Pen. 3: 263. 1924; Whitmore, Tree Flora Malaya 2: 134. 1973; Airy Shaw, Kew Bull. Add. Ser. 4: 201. 1975; Kew Bull. 36: 350. 1981. TYPE: *Trigonopleura malayana* Hook. f.

A monotypic genus of southeast Asia (Malaya to the Philippines and Borneo).

92. Chaetocarpus Thwaites, Hook. J. Bot. Kew Gard. Misc. 6: 300, t. 10a. 1854 (nom. cons.); Muell. Arg., DC. Prodr. 15(2): 1121. 1866; Bentham, Gen. Pl. 3: 323. 1880; Pax & Hoffm., Pflanzenr. 147. IV (Heft 52): 7. 1912; Fawc. & Rend., Fl. Jam. 4: 318. 1920; Pax & Hoffm., Natürl. Pflanzenfam. ed. 2, 19c: 179. 1931; Léonard, Fl. Congo 8(1): 127. 1962; Capuron, Adansonia II. 12: 209. 1972; Whitmore, Tree Fl. Malaya 2: 76. 1973. TYPE: *Chaetocarpus pungens* Thwaites [= *Chaetocarpus castanicarpus* (Roxb.) Thw.].

Mettenia Grisebach, Fl. Brit. W. Ind. 43. 1859. TYPE: *Mettenia globosa* Griseb. [= *Chaetocarpus globosus* (Griseb.) Fawc. & Rend.].

Regnaldia Baillon, Adansonia I. 1: 87. 1861. TYPE: *Regnaldia cluytioides* Baillon [= *Chaetocarpus castanicarpus* (Roxb.) Thw.].

Neochevaliera Beille, Compt. Rend. Hebd. Acad. Sci. Paris 145: 1295. 1907. TYPE: *Neochevaliera brazzavillensis* Beille [= *Chaetocarpus africanus* Pax].

A genus of 12 species with a disjunct distribution: West Indies, South America, west Africa, Madagascar, and tropical Asia.

Tribe 16. PEREAE (Kl. & Gcke.) Pax & Hoffmann, Pflanzenr. 147. XIII (Heft 68): 1. 1919. Peraceae Kl. & Gcke., Monatsber. Konigl. Preuss. Akad. Wiss. Berlin 1859: 246. 1859. Acalypheae subtribe Perinae (Kl. & Gcke.) Pax, Natürl. Pflanzenfam. ed. 1, 3(5): 69. 1890. TYPE: *Pera* Mutis.

Prosopidoclineae Klotzsch, Arch. Naturgesch. 7: 176. 1841. TYPE: *Pera* Mutis.

Dioecious trees or shrubs; indumentum simple, stellate, or lepidote; leaves alternate (rarely opposite), entire, pinnately veined, exstipulate. Flowers in axillary involucrate glomerules; involucre usually of 2 valvate bracts entirely enclosing flowers in bud. Flowers apetalous, disk absent; staminate calyx 2–4-fid or rudimentary; stamens 2–8, filaments connate; pollen grains 3-colporate, rugulose; pistillodes (representing reduced pistillate flowers) surrounding staminate flower. Pistillate flower without perianth; ovary 3-locular; styles stigmatiform. Fruit capsular, valves woody; seeds smooth, dark, carunculate; endosperm copious; cotyledons much longer and broader than radicle.

This tribe, by the unanimous consensus of workers since Baillon, includes only the single genus *Pera*. The relationships of *Pera* have been in doubt, however, because of the reduced nature of the flowers and the peculiar inflorescences that have no counterpart elsewhere in the family. Mueller (1866) placed *Pera* at the end of the Acalypheae (Acalyphoideae), Bentham (1880) at the end of the Hippomaneae, and Pax & Hoffmann (1922) following Dalechampieae. Airy Shaw (Dict. Fl. Pl. ed. 7, xxii. 1966) recognized Peraceae as a distinct family, but without discussion of its affinities. I believe that the closest relationship of *Pera* may be with tribe Chaetocarpeae, as indicated by similarity in the pollen and also the woody capsules with smooth carunculate seeds.

93. Pera Mutis, Kongl. Vetensk. Akad. Nya Handl. 5: 299. 1784; Muell. Arg., DC. Prodr. 15(2): 1025. 1866; Fl. Bras. 11(2): 421. 1874; Bentham, Gen. Pl. 3: 340. 1880; Pax & Hoffm., Pflanzenr. 147. XIII (Heft 68): 2. 1919; Jablonski, Mem. New York Bot. Gard. 17: 147. 1967. *Perula* Schreber, Gen. Pl. 703. 1791. TYPE: *Pera arborea* Mutis.

Spixia Leandro de Sacrameto, Denkschr. Königl. Akad. Wiss. München, Math. Phys. 7: 231. 1821 (non Schrank, 1821). TYPE: *Spixia heteranthera* Schrank [= *Pera heteranthera* (Schrank) I. M. Johnston].

Schismatopera Klotzsch, Arch. Naturgesch. 7: 178. 1841. TYPE: *Schismatopera martiana* Kl. [= *Pera distichophylla* (Mart.) Baillon].

A neotropical genus of ca. 30 species, extending from Cuba and Central America south to Brazil, with the greatest concentration of taxa in the Amazon basin.

Tribe 17. CHEILOSEAE (Muell. Arg.) Airy Shaw & Webster, Taxon 24: 595. 1975. Hippomaneae subtribe Cheiloseae Muell. Arg., Linnaea 34: 202. 1865. Gelonieae subtribe Chaetocarpinae series Cheilosiformes Pax & Hoffm., Pflanzenr. 147. XIV (Heft 68): 50. 1919. TYPE: *Cheilosa* Blume.

Dioecious trees; indumentum simple, stellate, or

nearly absent; leaves alternate, simple, entire or crenulate, penninerved, glandular or eglandular; stipules caducous; inflorescences axillary or sometimes terminal, paniculate, bracts eglandular; flowers apetalous; sepals 4 or 5, imbricate; staminate disk dissected, intrastaminal or extrastaminal; stamens 4–10, free; anthers muticous, introrse; pollen grains globose, 3-colporate, colpi inoperculate, exine echinate; pistillode present; pistillate disk annular or absent; ovary 2–3-locular; styles bifid; fruit capsular; seeds ecarunculate, testa fleshy; cotyledons longer and broader than radicle.

This tribe includes two genera, but has a different circumscription from the "series" Cheilosiformes of Pax & Hoffmann (1919, 1931), since *Elaeriospermum* is assigned to the subfamily Crotonoideae, and *Neoscortechinia* is added. Airy Shaw (1972) appears to have been the first to suggest that *Neoscortechinia* should be placed in the same tribe as *Cheilosa*.

KEY TO THE GENERA OF TRIBE CHEILOSEAE

1a. Fruit thick-walled, capsular, with 3 seeds; indumentum simple; stamens 8–10 _____ 94. *Cheilosa*
1b. Fruit thin-walled, with 1 seed; indumentum stellate; stamens 5 or 6 _____ 95. *Neoscortechinia*

94. Cheilosa Blume, Bijdr. 613. 1826; Muell. Arg., DC. Prodr. 15(2): 1122. 1866; Bentham, Gen. Pl. 3: 322. 1880; J. J. Sm., Add. Cogn. Fl. Arb. Jav. 12: 604. 1910; Pax & Hoffm., Pflanzenr. 147. IV (Heft 52): 12. 1912; Airy Shaw, Kew Bull. 16: 364. 1963; Whitmore, Tree Fl. Malaya 2: 77. 1973; Airy Shaw, Kew Bull. Add. Ser. 4: 68. 1975; Kew Bull. 36: 276. 1981. TYPE: *Cheilosa montana* Blume.

A genus of two species (perhaps conspecific) in southeast Asia (Malaya to the Philippines and Borneo).

95. Neoscortechinia Pax, Natürl. Pflanzenfam. Nachtr. 1: 213. 1897; Pax & Hoffm., Pflanzenr. 147. XIV (Heft 68): 52. 1919; Airy Shaw, Kew Bull. 16: 368. 1963; Whitmore, Tree Fl. Malaya 2: 119. 1973; Airy Shaw, Kew Bull. 36: 333. 1981. *Scortechinia* Hook. f., Hook. Ic. Pl. 18: t. 1706. 1887 (non *Scortechinia* Saccardo, 1885). TYPE: *Scortechinia kingii* Hook. f. [= *Neoscortechinia kingii* (Hook. f.) Pax & Hoffm.].

Alcinaeanthus Merrill, Phil. J. Sci. Bot. 7: 379. 1912. TYPE: *Alcinaeanthus philippinensis* Merr. [= *Neoscortechinia forbesii* Hook. f.) Pax ex S. Moore].

A tropical Asian genus of four species, distributed from Burma to the Philippines and Solomon Islands.

Tribe 18. ERISMANTHEAE Webster, Taxon 24: 595. 1975. TYPE: *Erismanthus* Wall. ex Muell. Arg.

Monoecious trees or shrubs; indumentum simple; leaves opposite, subsessile, simple, entire or obscurely dentate, basally oblique, penninerved, stipulate; inflorescences axillary, racemose or spicate; staminate sepals 4 or 5, imbricate or nearly valvate; petals 5; disk absent; stamens 5–15, filaments free; anthers muticous, introrse; pollen grains 3-colporate, angulaperturate, colpi inoperculate, not marginate, sexine reticulate; pistillode present; pistillate sepals 5–6, imbricate; petals present or absent; disk absent; ovary 3-locular; ovules anatropous; styles free to connate, entire or bifid; fruit capsular; seeds smooth, ecarunculate, testa dry.

This tribe includes three tropical Asian genera that share some common features with tribe Epiprineae. *Erismanthus* and *Moultonianthus* have a distinctive habit due to the opposite phyllotaxy and oblique leaf bases; this is present, but less pronounced, in *Syndyophyllum*.

KEY TO THE GENERA OF TRIBE ERISMANTHEAE

1a. Pistillode in staminate flower greatly elongated, clavate; young staminate inflorescence covered with closely imbricate bracts; pistillate flowers apetalous; staminate petals shorter than calyx; stamens 12–15 _____ 96. *Erismanthus*
1b. Pistillode not greatly elongated; young staminate inflorescences not covered with densely imbricate bracts; stamens 5–10.
2a. Styles distinctly bifid; staminate petals longer than calyx; pistillate flowers petaliferous; stipules persistent, foliaceous, and clasping _____ 97. *Moultonianthus*
2b. Styles entire or nearly so; staminate petals shorter than sepals; pistillate flowers apetalous; stipules small, deciduous _____ 98. *Syndyophyllum*

96. Erismanthus Wallich ex Muell. Arg., DC. Prodr. 15(2): 1138. 1866; Bentham, Gen. Pl. 3: 325. 1880; Hook. f., Fl. Brit. Ind. 5: 405. 1887; Pax & Hoffm., Pflanzenr. 147. III (Heft 47): 33. 1911; Gagnep., Fl. Indochine 5: 464. 1926; Airy Shaw, Kew Bull. 26: 260. 1972; Whitmore, Tree Fl. Malaya 2: 95. 1973; Airy Shaw, Kew Bull. Add. Ser. 4: 110. 1975; Kew Bull. 36: 294. 1981. TYPE: *Erismanthus obliquus* Muell. Arg.

An Asian genus of two species, the type species

occurring from Thailand to Sumatra and Borneo, the other species (*E. sinensis* Oliver) in Indochina and Hainan.

97. Moultonianthus Merrill, Phil. J. Sci. Bot. 11: 70. 1916; Pax & Hoffm., Pflanzenr. 147. XIV (Heft 68): 41. 1919; Natürl. Pflanzenfam. ed. 2, 19c: 170. 1931; Steenis, Bull. Bot. Gard. Buitenz. III. 17: 404. 1948; Airy Shaw, Kew Bull. Add. Ser. 4: 176. 1975; Kew Bull. 36: 332. 1981. TYPE: *Moultonianthus borneensis* Merr. [= *Moultonianthus leembruggianus* (Boerl. & Koord.) Steenis].

A monotypic genus known only from Sumatra and Borneo.

98. Syndyophyllum Lauterbach & K. Schumann, Fl. Deutsche Schutzg. 403. 1901; Pax & Hoffm., Pflanzenr. 147. III (Heft 47): 104. 1911; Airy Shaw, Kew Bull. 14: 392. 1960; Hook Ic. Pl. 38: t. 3722. 1974; Kew Bull. Add. Ser. 4: 199. 1975; 8: 204. 1980. TYPE: *Syndyophyllum excelsum* Lauterb. & K. Sch. [lectotype].

A monotypic genus, the single variable species found in Sumatra, Borneo, and New Guinea.

Tribe 19. DICOELIEAE Hurusawa, J. Fac. Sci. Univ. Tokyo Sect. 3, Bot. 6: 322. 1954; Webster, Bot. J. Linn. Soc. 94: 6. 1987. TYPE: *Dicoelia* L.

Monoecious trees or shrubs; indumentum simple; leaves simple, entire, pinnately veined, eglandular; stipules caducous. Inflorescences bisexual, racemose. Staminate sepals 5, valvate or nearly so; petals 5, valvate, with 2 concavities opposite anthers; disk absent; stamens 5; filaments slightly connate to base of 3–5-fid pistillode; pollen grains 3-colporate, tectate. Pistillate sepals 5, valvate; petals 5, slightly imbricate; disk absent; ovary 3-locular; ovules 2 per locule, anatropous; styles free or nearly so, unlobed, slender. Fruit capsular; seeds ecarunculate.

A monogeneric tribe, referred to subfamily Phyllanthoideae by Pax & Hoffmann (1922) because of the biovulate carpels. Although Airy Shaw (1981) suggested an affinity to *Trigonostemon* in the Crotonoideae, Bentham's original suggestion of a relationship to the Galearieae seems perceptive and best supported by the available data.

In my last review of the placement of *Dicoelia* (Webster, 1987), the tribe Dicoelieae was referred to the family Pandaceae as one of its two tribes, the other being the Galearieae. If the Euphorbiaceae were to be subdivided into segregate families, this arrangement still seems logical. However, in the present synopsis, where a broad concept of the family is taken, it appears necessary to include the Dicoelieae in the Acalyphoideae adjacent to the Galearieae. It might be possible to recognize a separate subfamily for the tribes Dicoelieae and Galearieae, but this seems premature until phylogenetic relationships within the subfamily Acalyphoideae are much better understood.

99. Dicoelia Bentham, Hook. Ic. Pl. 13: 70, t. 1289. 1879; Gen. Pl. 3: 286. 1880; J. J. Smith, Bull. Jard. Bot. Buitenz. III. 1: 392. 1920; Pax & Hoffm., Pflanzenr. 147. XII (Heft 81): 15. 1922; Croizat, J. Arnold Arbor. 23: 38. 1942; Airy Shaw, Kew Bull. 27: 3. 1972; 36: 285. 1981. TYPE: *Dicoelia beccariana* Benth.

A monotypic genus of Malaya, Sumatra, and Borneo according to Airy Shaw (1981), who does not accept *D. affinis* J. J. Sm. as distinct.

Tribe 20. GALEARIEAE Bentham, Gen. Pl. 3: 247, 287. 1880. Cluytieae subtribe Galearïinae Pax, Natürl. Pflanzenfam. ed. 1, 3(5): 81. 1890. TYPE: *Galearia* Zoll. & Mor.

Bennettiaceae R. Brown, Pl. Jav. Rar. 250. 1850 (nom. prov.). Bennettieae R. Brown ex Schnizlein, Iconogr. Fam. Nat. Regni Vegetab. 3: 172. 1860. TYPE: *Bennettia* R. Brown [non *Bennettia* S. F. Gray, 1821; = *Galearia* Zoll. & Mor.].

Pandaceae Pierre, Bull. Soc. Linn. Paris 1255. 1896; Engler & Gilg, Syll. Pflanzenfam. ed. 7, 223. 1913; Forman, Kew Bull. 20: 309. 1966; Webster, Bot. J. Linn. Soc. 94: 6. 1987. TYPE: *Panda* Pierre.

Dioecious trees or shrubs; indumentum simple; leaves alternate, simple, entire or dentate, pinnately veined, eglandular, stipulate. Inflorescences terminal thyrses or axillary glomerules; bracts sometimes persistent. Staminate sepals free or connate, slightly imbricate or valvate; petals valvate or somewhat imbricate, with ventral paired depressions opposite anthers; disk absent; stamens 5–15, free; anthers introrse; pistillode unlobed, sometimes peltate; pollen grains subglobose, angulaperturate, 3-colporate, sexine finely reticulate. Pistillate sepals free or connate; petals valvate; ovary mainly 3-(2–5-)locular; ovules 1 per locule, anatropous or orthotropous; styles bifid or multifid. Fruit drupaceous; exocarp fleshy or woody; endocarp bony and corrugated or channeled; seeds ecarunculate, endosperm copious.

The tribe Galearieae as treated here corresponds exactly, except for rank, with the family Pandaceae

as circumscribed by Forman (1966). The group has had a rather complicated taxonomic history, which Forman has discussed thoroughly as far as *Panda* is concerned. Bentham (1878, 1880) perceptively noted the resemblance of *Dicoelia* with *Galearia*, even though he retained *Dicoelia* in the Phyllantheae (no doubt because of its biovulate carpels). His tribe Galearieae, proposed rather apologetically as a transitional group between Phyllantheae and Crotoneae, included *Galearia* and *Microdesmis* juxtaposed.

The Pandaceae have generally been accepted in the 20th century as a distinct family, usually with a position next to the Euphorbiaceae (e.g., Cronquist, 1981; Radcliffe-Smith, 1987). In my previous review of the group (Webster, 1987), Pandaceae was expanded to include the tribe Dicoelieae (previously situated in subfamily Phyllanthoideae). Whatever their eventual disposition, it appears that Dicoelieae and Galearieae (as here defined) form a coherent and apparently monophyletic group.

The key to the three genera follows that of Forman.

KEY TO THE GENERA OF TRIBE GALEARIEAE

1a. Inflorescences axillary, flowers solitary or in glomerules; staminate petals imbricate; leaves usually pellucid-punctate ..... 100. *Microdesmis*

1b. Inflorescences terminal or cauliflorous, thyrsoid; staminate petals valvate or nearly so; leaves not pellucid-punctate.

2a. Endocarp thin-walled; ovules usually anatropous; petals valvate; inflorescences mostly terminal ..... 101. *Galearia*

2b. Endocarp thick-walled; ovules orthotropous; petals ± imbricate; inflorescences cauliflorous ..... 102. *Panda*

100. Microdesmis Planchon, Hook. Ic. Pl. 8: t. 758. 1848; Muell. Arg., DC. Prodr. 15(2): 1041. 1866; Bentham, Gen. Pl. 3: 287. 1880; Pax & Hoffm., Plfanzenr. 147. III (Heft 47): 105. 1911; Gagnepain, Fl. Indochine 5: 458. 1926; Léonard, Bull. Jard. Bot. Brux. 31: 159. 1961; Fl. Congo 8(1): 102. 1962; Whitmore, Tree Fl. Malaya 2: 118. 1973; Airy Shaw, Kew Bull. Add. Ser. 4: 222. 1975. TYPE: *Microdesmis puberula* Hook. f. ex Planch.

A paleotropical genus of ten species, eight African and two Asian.

101. Galearia Zollinger & Moritzi, Syst. Verz. 19. 1846 (nom. cons. prop.); Muell. Arg., DC. Prodr. 15(2): 1036. 1866; Bentham, Gen. Pl. 3: 287. 1880; Hook. f., Fl. Brit. Ind. 5: 377. 1887; Pax & Hoffm., Pflanzenr. 147. III (Heft 47): 97. 1911; Gagnepain, Fl. Indochine 5: 456. 1926; Forman, Kew Bull. 26: 155. 1971; Whitmore, Tree Fl. Malaya 2: 97. 1973. TYPE: *Galearia sessilis* Zoll. & Mor. [= *Galearia filiformis* (Bl.) Boerl.; lectotype selected here because the other species of Zollinger & Moritzi, *G. pedicellata*, could be confused with *Bennettia pedicellata* R. Br.].

Cremostachys Tulasne, Ann. Sci. Nat. III. 15: 259. 1851. TYPE: *Cremostachys filiformis* (Bl.) Tul. [= *Galearia filiformis* (Bl.) Boerl.; lectotype].

Bennettia R. Brown, Pl. Jav. Rar. 249. 1852 (non S. F. Gray, 1821). TYPE: *Bennettia javanica* R. Br. [= *Galearia filiformis* (Bl.) Boerl.].

As treated by Forman (1971), *Galearia* includes six species of tropical southeast Asia (Burma to Solomon Islands).

102. Panda Pierre, Bull. Mens. Soc. Linn. Paris 1255. 1896; Aubréville, For. Fl. Côte Iv. 1: 300. 1959; Keay, Fl. W. Trop. Afr., ed. 2, 1: 634. 1958; Forman, Kew Bull. 20: 309. 1966. TYPE: *Panda oleosa* Pierre.

Porphyranthus Engler, Bot. Jahrb. Syst. 26: 367. 1899. TYPE: *Porphyranthus zenkeri* Engler [= *Panda oleosa* Pierre].

A monotypic genus of west tropical Africa. Although *Panda* diverges from nearly all other Euphorbiaceae in its distinctive characters (e.g., orthotropous ovules), Forman appears correct in seeing it as the terminus of a sequence of morphological changes within the Galearieae.

Tribe 21. AMPEREAE Muell. Arg., Bot. Zeit. 22: 324. 1864; DC. Prodr. 15(2): 211. 1866. TYPE: *Amperea* A. Juss.

Ampereae subtribe Monotaxideae Muell. Arg., Linnaea 34: 63. 1865. TYPE: *Monotaxis* Brongn.

Monoecious (rarely dioecious) herbs or subshrubs; indumentum simple; leaves alternate, ericoid, stipulate; flowers in terminal or axillary glomerules; staminate calyx 3–5-lobed, lobes valvate or slightly imbricate; petals present or absent; disk entire or dissected; stamens 6–10, biseriate, filaments free, anthers with disjunct or pendulous loc-ules; pollen grains 3-colporate, colpi inoperculate, distinctly marginate, sexine perforate-tectate; pistillode present or absent; pistillate sepals 4 or 5, imbricate or valvate; petals small or absent; disk annular, dissected, or absent; ovary 3-locular; styles bifid to multifid; fruit capsular; seeds smooth, ca-

runculate; endosperm copious; embryo cylindric, cotyledons scarcely broader than radicle.

In the circumscription of Pax (1890) and Grüning (1913), which is followed here, tribe Ampereae includes two genera confined to Australia. Although the pollen grains are similar in exine sculpturing and marginate colpi, the genera are dissimilar in many ways, and it is not certain that they should be associated in the same tribe.

KEY TO THE GENERA OF TRIBE AMPEREAE

1a. Staminate petals present; sepals imbricate; anther locules disjunct; pollen grains 3-angled, sexine reticulate; style-branches fimbriate; cymes terminal ..... 103. *Monotaxis*

1b. Staminate petals absent; sepals valvate; anther locules pendulous from glandular connective; pollen grains 3-lobed, sexine perforate-foveolate; style-branches entire; flowers axillary ..... 104. *Amperea*

103. Monotaxis Brongniart, Voy. Coquille Bot. 223. 1829; Muell. Arg., DC. Prodr. 15(2): 212. 1866; Bentham, Fl. Austral. 6: 78. 1873; Gen. Pl. 3: 264. 1880; Grüning, Pflanzenr. 147. (Heft 58): 75. 1913; Pax & Hoffm., Natürl. Pflanzenfam. ed. 2, 19c: 227. 1931; Airy Shaw, Muelleria 4: 239. 1980. TYPE: *Monotaxis linifolia* Brongn. [lectotype].

Hippocrepandra Muell. Arg., Linnaea 34: 61. 1865. TYPE: *Hippocrepandra gracilis* Muell. Arg. [= *Monotaxis lurida* (Muell. Arg.) Benth.; lectotype, designated by Wheeler, 1975].

An Australian genus of about ten species. Brongniart, in his original description, suggested an affinity to *Chiropetalum* and *Ditaxis* in tribe Chrozophoreae. Punt (1962) related pollen of *Monotaxis* to his "Sumbavia type," which includes genera of tribe Chrozophoreae. Perhaps further study will demonstrate that *Monotaxis* is indeed an aberrant genus of Chrozophoreae.

104. Amperea A. Jussieu, Euphorb. Tent. 35. 1824; Muell. Arg., DC. Prodr. 15(2): 213. 1866; Bentham, Fl. Austral. 6: 81. 1873; Gen. Pl. 3: 265. 1880; Grüning, Pflanzenr. 147 (Heft 58): 86. 1913; Pax & Hoffm., Natürl. Pflanzenfam. ed. 2, 19c: 228. 1931; Henderson, Austral. Syst. Bot. 10 (in press). 1993. TYPE: *Amperea ericoides* A. Juss.

According to Henderson (1993), *Amperea* is a genus of eight Australian species, all except two confined to Western Australia. On the basis of pollen characters, Punt (1962) related *Amperea* to genera in tribe Epiprineae; this suggestion merits further inquiry.

Tribe 22. AGROSTISTACHYDEAE (Muell. Arg.) Webster, Taxon 24: 596. 1975. Acalypheae subtribe Agrostistachydeae Muell. Arg., Linnaea 34: 143. 1865. TYPE: *Agrostistachys* Dalz.

Dioecious (rarely monoecious) trees or shrubs; indumentum simple or absent; leaves alternate, simple, entire or denticulate, lamina glandular or eglandular; stipules persistent or deciduous; inflorescences axillary, racemose or spicate, sometimes with scarious imbricate bracts; staminate calyx closed in bud, splitting into 2–5 valvate lobes; petals 3–8; disk receptacular or extrastaminal and dissected; stamens 10–50, filaments free (at least in part), anthers introrse, with ± enlarged connective, anther-sacs often pendulous; pollen grains subglobose, 3-colporate, colpi inoperculate, not distinctly marginate, sexine coarsely reticulate; pistillode present or absent; pistillate sepals 4 or 5, open or valvate; petals 5, small and deciduous, or absent; disk lobed, pitted, or dissected; ovary 3-locular, often tomentose; styles bifid; fruit capsular; seeds smooth or granulose, ecarunculate, testa sometimes fleshy.

This tribe is here considered to include four genera, two African and two Asiatic.

KEY TO THE GENERA OF TRIBE AGROSTISTACHYDEAE

1a. Petals present; flowers in spikes or racemes.
  2a. Dioecious; staminate petals imbricate in bud; petals present in pistillate flower.
    3a. Staminate disk dissected; stamens 8–10; stipules free; leaves eglandular ..... 105. *Agrostistachys*
    3b. Staminate disk receptacular; stamens 20–55; stipules connate, leaving an annular scar; leaves glandular at base ..... 106. *Pseudagrostistachys*
  2b. Monoecious; staminate petals not imbricate in bud; pistillate flowers apetalous; leaves glandular at base ..... 107. *Cyttaranthus*

1b. Petals absent; flowers in panicles; monoecious, leaves glandular at base ..... 108. *Chondrostylis*

105. Agrostistachys Dalzell, Hook. J. Bot. Kew Gard. Misc. 2: 41. 1850; Muell. Arg., DC. Prodr. 15(2): 725. 1866; Bentham, Gen. Pl. 3: 302. 1880; Hook. f., Fl. Brit. Ind. 5: 405. 1887; Pax & Hoffm., Pflanzenr. 147. VI (Heft 57): 98. 1912; Gagnep., Fl. Indochine 5: 463. 1926; Airy Shaw, Kew Bull. 14: 472. 1960; 26: 210. 1972; Whitmore, Tree Fl. Malaya 2: 52. 1973; Airy Shaw, Kew Bull. Add. Ser.

4: 26. 1975; Kew Bull. 36: 248. 1981. TYPE: *Agrostistachys indica* Dalz.

Heterocalyx Gagnepain, Notul. Syst. (Paris) 14: 33. 1950. TYPE: *Heterocalyx laoticus* Gagnep. [= *Agrostistachys indica* Dalz.].

An Asiatic genus of ten species, some difficult to distinguish, distributed from India and Sri Lanka to New Guinea.

106. Pseudagrostistachys Pax & Hoffmann, Pflanzenr. 147. VI (Heft 57): 96. 1912; Lebrun, Bull. Soc. Roy. Belge 67: 97. 1934; Léonard, Fl. Congo 8(1): 183. 1962; Radcliffe-Smith, Fl. E. Trop. Afr. Euphorb. 1: 166. 1987. TYPE: *Pseudagrostistachys africana* (Muell. Arg.) Pax & Hoffm.

An African genus of two species distributed from São Tome and Nigeria to Zaire and Uganda.

107. Cyttaranthus Léonard, Bull. Jard. Bot. Brux. 25: 286. 1955; Fl. Congo 8(1): 180. 1962. TYPE: *Cyttaranthus congolensis* Léonard.

A monotypic genus confined to west Africa (Congo and Cabinda); extremely close to *Chondrostylis* and perhaps not separable.

108. Chondrostylis Boerlage, Ic. Bogor. 1: t. 23. 1897; Koorders, Ann. Jard. Bot. Buitenz. 19: 45. 1904; Pax & Hoffm., Pflanzenr. 147. VII (Heft 63): 15. 1914; Airy Shaw, Kew Bull. 14: 358. 1960; Whitmore, Tree Fl. Malaya 2: 77. 1973; Airy Shaw, Kew Bull. Add. Ser. 4: 69. 1975; Kew Bull. 36: 276. 1981. TYPE: *Chondrostylis bancana* Boerl.

Kunstlerodendron Ridley, Fl. Malay Penn. 3: 283. 1924. TYPE: *Kunstlerodendron sublanceolata* Ridl., nom. illeg. [= *Chondrostylis kunstleri* (King ex Hook. f.) Airy Shaw].

A monotypic genus of southeast Asia (Thailand to Sumatra and Borneo).

Tribe 23. CHROZOPHOREAE (Muell. Arg.) Pax & Hoffmann, Pflanzenr. 147. XIV (Heft 68): 5. 1919. Chrozophoreae subtribe Regulares (Pax & Hoffm.) Pax & Hoffm., Natürl. Pflanzenfam. ed. 2, 19c: 89. 1931. TYPE: *Chrozophora* Necker ex A. Juss.

Trees, shrubs, or herbs, monoecious or dioecious; indumentum usually stellate, lepidote, or malpighiaceous (at least in part; rarely entirely simple); leaves alternate, unlobed or lobed, entire or dentate, pinnately or palmately veined, sometimes with laminar glands; stipules persistent or deciduous, sometimes obsolete; inflorescences axillary or terminal, mostly racemose or spicate. Staminate flower: sepals 3–5, valvate; petals 4 or 5 (rarely 10 or absent); disk dissected or absent; stamens 5–many, filaments free or connate; anthers introrse, muticous, locules not pendulous; pollen grains subglobose to oblate, mostly 3-6-colporate, colpi sometimes operculate, not distinctly marginate, sexine reticulate, often distinctly heterobrochate; pistillode present or absent. Pistillate flower: sepals 5 or 6, imbricate or valvate; petals 5 (sometimes reduced or absent); disk annular or dissected (rarely absent); ovary (2-)3-locular, smooth or muricate; styles unlobed to bifid or twice-bifid, sometimes lacerate. Fruit capsular; seeds dry or fleshy, endotesta smooth or roughened to pitted, ecarunculate.

As delimited by Webster (1975) and here, tribe Chrozophoreae corresponds almost exactly to the subtribe Regulares as treated by Pax & Hoffmann (1931); their other subtribe Irregulares includes genera belonging to tribe Agrostistachydeae and subfamily Crotonoideae. Pollen characters in genera such as *Doryxylon* suggest a possible relationship between Chrozophoreae and tribe Epiprineae.

KEY TO THE SUBTRIBES OF TRIBE CHROZOPHOREAE

1a. Pollen grains not distinctly heterobrochate; indumentum simple or malpighiaceous; leaves not with basal laminar glands.
  2a. Inflorescences terminal; indumentum entirely simple; stamens 10–15, free; pistillate disk annular; ovary muricate ——— 23a. Speranskiinae
  2b. Inflorescences axillary; indumentum malpighiaceous or stellate (at least in part); stamens, if more than 6, connate; pistillate disk dissected or obsolete ——— 23b. Ditaxinae
1b. Pollen grains distinctly heterobrochate; indumentum stellate; leaves with basal laminar glands.
  3a. Shrubs or trees; pollen grains 3-colporate; stamens free; seeds fleshy ——— 23c. Doryxylinae
  3b. Herbs; pollen grains stephanocolporate; stamens connate; seeds not fleshy ——— 23d. Chrozophorinae

Subtribe 23a. SPERANSKIINAE Webster. Taxon 24: 596. 1975. TYPE: *Speranskia* Baillon.

Monoecious herbs; indumentum simple; leaves alternate, coarsely dentate or lobulate, with glandular teeth, stipulate; inflorescences terminal, spicate, bisexual, pistillate flowers proximal; staminate sepals and petals 5; disk dissected; stamens 10–15

filaments free; pollen grains 3-colporate, evenly reticulate; pistillode absent; pistillate sepals 5; petals 5, small or absent; disk annular; ovary 3-locular, verrucose; styles free, bifid, branches lacerate; fruit capsular; seeds dry, ecaruncuIate, testa foveolate-asperate.

This monogeneric subtribe is morphologically similar to subtribe Ditaxinae, and indeed Mueller (1866) included *Speranskia* as a section of *Argythamnia*. However, the Speranskiinae diverge from the Ditaxinae in a number of characters, particularly the androecium of free stamens and the terminal inflorescence.

109. Speranskia Baillon, Etude Gén. Euphorb. 388. 1858; Bentham, Gen. Pl. 3: 305. 1880; Pax & Hoffm., Pflanzenr. 147. VI (Heft 57): 14. 1912; Hurusawa, J. Fac. Sci. Univ. Tokyo III. Bot. 6: 310. 1954. TYPE: *Speranskia tuberculata* (Bunge) Baillon.

A genus restricted to China; there are three species according to Pax & Hoffmann (1912) or two according to Hurusawa (1954).

Subtribe 23b. DITAXINAE Grisebach, Fl. Brit. W. Ind. 43. 1859; Abh. Gesell. Wiss. Goettingen 9: 15. 1861. TYPE: *Ditaxis* Vahl ex A. Juss.

Acalypheae subtribe Caperonieae Muell. Arg., Linnaea 34: 143. 1865. TYPE: *Caperonia* St. Hil.

Monoecious (rarely dioecious) trees, shrubs, or herbs; indumentum predominantly malpighiaceous, sometimes also stellate, simple, or glandular; leaves alternate, entire or serrate, without laminar glands; inflorescences axillary, racemose or glomerulate, usually bisexual; staminate sepals mostly 4 or 5; petals 4 or 5; disk dissected or absent; stamens 4–15, filaments connate (rarely almost free); anthers introrse; pollen grains subglobose to oblate, 3-colporate to stephanocolporate, sexine reticulate, not distinctly heterobrochate; pistillode present or absent; pistillate sepals 5 or more, imbricate to valvate, petals 5(6), sometimes obsolete; disk dissected or absent; ovary sometimes muricate; styles bifid to laciniate; fruit capsular; seeds dry, smooth or ornamented (foveolate, asperate, or reticulate), ecaruncuIate.

In the circumscription of Webster (1975), which is continued here, subtribe Ditaxinae includes five genera that are confined to the New World except for a few species of *Caperonia*. The subtribe approaches subtribe Speranskiinae via *Caperonia*, which resembles the Chinese genus in its muricate ovary and laciniate style-branches, but differs in its axillary racemes and stephanocolporate pollen. Generic delimitation within the subtribe is still controversial, but pollen characters such as pointed out by Punt (1962) support the narrow circumscription of Pax & Hoffmann rather than the broad delimitation of Mueller (1866) and Ingram (1979).

KEY TO THE GENERA OF SUBTRIBE DITAXINAE

1a. Pistillode present; styles dissected, indumentum simple or glandular (not malpighiaceous), leaves finely serrate with straight parallel lateral veins, pollen grains 6-colporate ..... 110. *Caperonia*

1b. **Pistillode absent; styles bifid to dissected;** indumentum (at least in part) malpighiaceous, leaves otherwise; pollen grains 3- or 4-colporate

2a. Dioecious; tepals scarious; shrubs or trees, branches often spiny ..... 111. *Philyra*

2b. Monoecious; tepals not scarious, undershrubs or herbs, not spiny.

3a. Petals entire; styles twice bifid to multifid; stellate hairs absent.

4a. Stamens 8–10, anthers in 2 whorls; pollen grains 3- or 4-colporate, bilaterally symmetrical ..... 112. *Ditaxis*

4b. Stamens 4 or 5, anthers in 1 whorl; pollen grains stephanocolporate ..... 113. *Argythamnia*

3b. Petals toothed or lacerate; styles once bifid; stellate hairs sometimes present; pollen grains 3-colporate ..... 114. *Chamaetalum*

110. Caperonia St. Hilaire, Pl. Remarq. Bresil 244. 1826; Muell. Arg., DC. Prodr. 15(2): 751. 1866; Fl. Bras. 11(2): 315. 1874; Bentham, Gen. Pl. 3: 304. 1880; Pax & Hoffm., Pflanzenr. 147. VI (Heft 57): 27. 1912; Léonard, Bull. Jard. Bot. Brux. 26: 313. 1956, Fl. Congo 8(1): 166. 1962, Webster, J. Arnold Arbor. 48: 363. 1967, Dyer, Gen. S. Afr. Fl. Pl. 1: 314. 1975; Radcliffe-Smith, Fl. E. Trop. Afr. Euphorb. 1: 163. 1987. TYPE: *Caperonia castaneifolia* (L.) St. Hil. [lectotype, designated by Britton & Wilson, Bot. Porto Rico 6: 486. 1925].

A genus of ca. 40 species, mostly American, less than 10 species in Africa. *Caperonia* is quite sharply distinct from the other genera in subtribe Ditaxinae, and Mueller referred it to a separate subtribe Caperonieae. On the basis of present reports (Hans, 1973), *Caperonia* appears to have a different chromosome number (x = 11) from the other genera (x = 13).

111. Philyra Klotzsch, Arch. Naturgesch. 7(1): 199. 1841; Baillon, Etude Gén. Euphorb. 297.

1858; Pax & Hoffmann, Pflanzenr. 147. VI (Heft 57): 49. 1912; Natürl. Pflanzenfam. ed. 2, 19c: 92. 1931; O'Donell & Lourteig, Lilloa 8: 60. 1942. TYPE: *Philyra brasiliensis* Kl.

A monotypic genus of Paraguay and southern Brazil.

112. Ditaxis Vahl ex A. Jussieu, Euphorb. Tent. 27. 1824; Pax, Natürl. Pflanzenfam. ed. 1, 3(5): 44. 1890; Pax & Hoffm., Pflanzenr. 147. VI (Heft 57): 51. 1912; Natürl. Pflanzenfam. ed. 2, 19c: 93. 1931. TYPE: *Ditaxis fasciculata* Vahl ex A. Juss.

Aphora Nuttall, Trans. Amer. Phil. Soc. II. 5: 174. 1837. TYPE: *Aphora mercurialina* Nutt. [= *Ditaxis mercurialina* (Nutt.) Coulter].

Serophyton Bentham, Bot. Voy. Sulphur 52. 1844. TYPE: *Serophyton lanceolatum* Benth. [= *Ditaxis lanceolata* (Benth.) Pax & Hoffm.].

Stenonia Didrichsen, Vidensk. Medd. Dansk Naturhist. Foren. Kjøbenhavn 1857f: 146. 1857 (non Endlicher, 1947). TYPE: *Stenonia montevidensis* Didr. [= *Ditaxis montevidensis* (Didr.) Pax].

Paxiuscula Herter, Rev. Sudamer. Bot. 6: 92. 1941. TYPE: *Paxiuscula acaulis* (Herter ex Arech.) Herter [= *Ditaxis acaulis* Herter].

An American genus of 40–50 species distributed in drier areas from the United States south to Argentina. *Ditaxis* is very close to *Argythamnia*, and it remains to be demonstrated whether it should be combined with that genus, as many workers, including Mueller (1866), Bentham (1880), and Ingram (1979), have proposed. However, evidence from pollen morphology (Punt, 1962; Webster, ined.) tends to support its status as a distinct genus.

113. Argythamnia P. Brown, Civ. Nat. Hist. Jamaica 338. 1756; Swartz, Fl. Ind. Occid. 1: 335. 1797; Muell. Arg., DC. Prodr. 15(2): 732. 1866; Bentham, Gen. Pl. 3: 303. 1880; Pax & Hoffm., Pflanzenr. 147. VI (Heft 57): 78. 1912; Johnston & Warnock, Southw. Nat. 7: 154. 1962; Ingram, Brittonia 16: 271. 1964; Gentes Herb. 10(1): 1–46. 1967; 11(7): 426. 1979; Correll & Correll, Fl. Bahama Arch. 777. 1982; Sneep & De Roon, Fl. Neth. Ant. 3: 250. 1984. TYPE: *Argythamnia candicans* Swartz.

In the revisional study by Ingram (1967), 18 species of *Argythamnia* (sensu stricto) are recognized. It is a Caribbean genus with over half the species in the West Indies, but a number also occurring in Mexico and Central America.

114. Chiropetalum A. Jussieu, Ann. Sci. Nat. I. 25: 21. 1832; Pax & Hoffm., Pflanzenr. 147. VI (Heft 57): 86. 1912; Ingram, Gentes Herb. 11(7): 437. 1979; L. Smith et al., Fl. Ilustr. Catar. EUFO 154. 1988. TYPE: *Chiropetalum tricuspidatum* (Lam.) A. Juss.

Desfontaena Vellozo, Fl. Flum. 95. 1825. TYPE: *Desfontaena tricocca* Vell. [= *Chiropetalum tricoccum* (Vell.) Chod. & Hassl.].

Chlorocaulon Kl. ex Endl., Gen. Pl. Suppl. 4(3): 89. 1850. TYPE: *Chiropetalum schiedeanum* (Muell. Arg.) Pax & Hoffm.

Aonikena Spegazzini, Anal. Mus. Nac. Hist. Nat. Buenos Aires II. 7: 162. 1902. TYPE: *Aonikena patagonica* Speg. [= *Chiropetalum patagonicum* (Speg.) O'Don. & Lourt.].

A genus of ca. 20 species, almost entirely in temperate South America except for a single Mexican species. Although reduced to a section of *Argythamnia* by Ingram, *Chiropetalum* is distinctive in its lobed petals and different pollen type (Punt, 1962).

Subtribe 23c. DORYXYLINAE Webster, Taxon 24: 596. 1975. TYPE: *Doryxylon* Zoll.

Monoecious shrubs or trees; indumentum stellate; leaves alternate, entire or dentate, with laminar glands; stipules small; inflorescences terminal or axillary, usually bisexual; staminate sepals 3–5; petals 5–10 or absent; disk reduced or absent; stamens many (ca. 30–250), free or partially connate; pollen grains 3-colporate, angulaperturate, coarsely reticulate, slightly heterobrochate along colpi; pistillode present or absent; pistillate sepals 5 or 6, imbricate or valvate; petals rudimentary or absent; disk annular (or obsolete); ovary 2- or 3-locular, stellate-pubescent; styles unlobed or bifid; seeds with fleshy exotesta, foveolate endotesta.

This subtribe of four Asian genera stands out from other Chrozophoreae by the combination of woody habit and stellate pubescence.

KEY TO THE GENERA OF SUBTRIBE DORYXYLINAE

1a. Petals present; ovary 3-locular; stamens ca. 30–100.
  2a. Inflorescences axillary; styles unlobed, basally connate; stamens free _ 115. *Doryxylon*
  2b. Inflorescences terminal; styles bifid, ± free.
    3a. Stamens free; staminate disk absent; pistillate sepals imbricate _____ 116. *Sumbaviopsis*
    3b. Stamens connate; staminate disk present; pistillate sepals valvate _____ 117. *Thyrsanthera*
1b. Petals absent; ovary usually 2-locular; stamens 200 or more; inflorescences terminal; styles entire _____ 118. *Melanolepis*

115. Doryxylon Zollinger, Tijdschr. Ned.-Indië 14: 172. 1857; Linnaea 29: 469. 1859; Ba-

lakrishnan, Bull. Bot. Surv. India 9: 56. 1967. TYPE: *Doryxylon spinosum* Zoll.

Sumbavia Baillon, Etude Gén. Euphorb. 390. 1858; Muell. Arg., DC. Prodr. 15(2): 727. 1866; Pax & Hoffm., Pflanzenr. 147. VI (Heft 57): 11. 1912. TYPE: *Sumbavia rottleroides* Baillon [= *Doryxylon spinosum* Zoll.].

This Asian genus, according to Balakrishnan, includes two species, but he treated *Sumbaviopsis* as a synonym of *Doryxylon*. He may be correct in this, but until the relationships can be further investigated, also taking *Thyrsanthera* into account, it seems best to provisionally keep the genera distinct. Earlier workers, from Mueller (1866) to Pax & Hoffmann (1912, 1931), used *Sumbavia* as the name for this genus because they thought *Doryxylon* was first published in *Linnaea* in 1859, and hence did not have priority.

116. Sumbaviopsis J. J. Smith, Add. Fl. Arb. Jav. 12 (Med. Dept. Landbouw 10): 356. 1910; Pax & Hoffm., Pflanzenr. 147. VI (Heft 57): 13. 1912; Gagnep., Fl. Indochine 5: 418. 1926; Airy Shaw, Kew Bull. 14: 357. 1960; Whitmore, Tree Fl. Malaya 2: 132. 1973; Airy Shaw, Kew Bull. Add. Ser. 4: 197. 1975. TYPE: *Sumbaviopsis albicans* (Bl.) J. J. Sm.

A monotypic tropical Asian genus (Assam to Borneo and Palawan).

117. Thyrsanthera Pierre ex Gagnepain, Bull. Soc. Bot. France 71: 878. 1925; Gagnepain, Fl. Indochine 5: 299. 1925; Pax & Hoffm., Natürl. Pflanzenfam. ed. 2, 19c: 90. 1931; Backer & Backh., Fl. Jav. 1: 477. 1963; Airy Shaw, Kew Bull. 19: 308. 1965; 26: 343. 1972. TYPE: *Thyrsanthera suborbicularis* Pierre ex Gagnep.

A monotypic genus known from Thailand and Cambodia. Airy Shaw (1972, in clavi) suggested that it may be more closely related to *Chrozophora* than to *Sumbaviopsis*.

118. Melanolepis Reichb. f. & Zoll., Verh. Natuurk. Ver. Ned. Ind. 1: 22. 1856; Linnaea 28: 324. 1856; Pax & Hoffm., Pflanzenr. 147. VII (Heft 63): 142. 1914; Gagnepain, Fl. Indochine 5: 347. 1925; Kanehira, Fl. Micronesica 180. 1933; Airy Shaw, Kew Bull. Add. Ser. 8: 174. 1980. TYPE: *Melanolepis multiglandulosa* (Reinw.) Reichb. f. & Zoll.

An Asian genus of two species extending from Thailand and Cambodia to Taiwan, Marianas, and Bismarck Archipelago.

Subtribe 23d. CHROZOPHORINAE Muell. Arg., Linnaea 34: 143. 1865; DC. Prodr. 15(2): 726. 1866; Pax & Hoffm., Pflanzenr. 147. VI (Heft 57): 1. 1912. TYPE: *Chrozophora tinctoria* (L.) A. Juss.

Monoecious herbs or subshrubs; indumentum stellate; leaves alternate, entire or lobed, biglandular at base, stipulate; inflorescences axillary, racemose, bisexual; staminate sepals and petals 5; disk inconspicuous, adnate to staminal column; stamens 4–15, filaments connate into a column; anthers introrse; pollen grains oblate, stephanocolporate, colpi short and broad, sexine distinctly heterobrochate; pistillode absent; pistillate sepals 5; petals 5, small or absent; disk lobed or dissected; ovary 3-locular, stellate or lepidote, sometimes muricate; styles bifid; fruit capsular; seeds caruncolate, somewhat fleshy, endotesta smooth or tuberculate.

In the present circumscription, subtribe Chrozophorinae is monogeneric. It is very close to subtribe Doryxylinae, as noted by Airy Shaw (1972, 1975), and further study may show that *Thyrsanthera* bridges the apparent gap between the two taxa.

119. Chrozophora Necker ex A. Jussieu, Euphorb. Tent. 27. 1824 (as *Crozophora*), nom. & orth. cons.; Muell. Arg., DC. Prodr. 15(2): 746. 1866; Bentham, Gen. Pl. 3: 305. 1880; Pax & Hoffm., Pflanzenr. 147. VI (Heft 57): 17. 1912; Prain, Kew Bull. Misc. Inf. 1918: 49. 1918; Pojarkova, Fl. URSS 14: 288. 1949; Rech. f. & Schiman-Czeika, Fl. Iranica 6: 5. 1964; Berhaut, Fl. Ill. Sénégal 3: 397. 1975; Radcliffe-Smith, Fl. E. Trop. Afr. Euphorb. 1: 160. 1987. TYPE: *Chrozophora tinctoria* (L.) A. Juss.

An Old World genus of ca. ten species distributed from southern Europe to east Africa, central and southern Asia.

Tribe 24. CARYODENDREAE Webster, Taxon 24: 596. 1975. TYPE: *Caryodendron* Karsten.

Dioecious trees or shrubs; indumentum simple; leaves alternate, penninerved or triplinerved, with basal glands; stipules persistent, reduced, or absent; inflorescences terminal or axillary, spicate. Flowers apetalous; staminate sepals 3–5, valvate; disk intrastaminal, pubescent; stamens 4–15, filaments free; anthers introrse, connective enlarged or glandular; pollen grains oblate, 3-colporate, colpi not marginate, sexine coarsely reticulate; pistillode

present or absent. Pistillate sepals 4–6, imbricate or valvate, deciduous; disk annular or dissected, pubescent; ovary 3-(rarely 2- or 4-)locular; styles free, unlobed. Fruit capsular; seeds ecarunculate, testa dry or fleshy.

This tribe of three genera is represented by two genera in the New World and one genus in Africa. The pollen grains are very similar to those in tribe Agrostistachydeae, which may be the most closely related taxon; however, they clearly differ from Caryodendreae in having petaliferous flowers, more stamens, a glabrous floral disk, and bifid styles.

KEY TO THE GENERA OF TRIBE CARYODENDREAE

1a. Pistillode absent; inflorescence terminal.
  2a. Staminate disk massive, pulviniform; capsule thick-walled, seed coat dry; leaves penninerved, stipules deciduous ..... 120. *Caryodendron*
  2b. Staminate disk dissected; capsule thin-walled, seed coat fleshy; leaves triplinerved, exstipulate ..... 121. *Discoglypremna*
1b. Pistillode present; inflorescences axillary; staminate disk massive, annular; capsule thin-walled; seed coat fleshy; leaves triplinerved, exstipulate ..... 122. *Alchorneopsis*

120. Caryodendron Karsten, Fl. Colombiae 1: 91, t. 45. 1860; Muell. Arg., Fl. Bras. 11(2): 706. 1874; Bentham, Gen. Pl. 3: 314. 1880; Pax & Hoffm., Pflanzenr. 147. VII (Heft 63): 263. 1914; Ducke, Trop. Woods 76: 18. 1943; Webster, Ann. Missouri Bot. Gard. 54: 287. 1968; Huft, Ann. Missouri Bot. Gard. 76: 1077. 1989. TYPE: *Caryodendron orinocense* Karst.

A neotropical genus of three species recorded from Panama to Colombia and Brazil. Huft (1989) has recently shown that *Centrodiscus* Muell. Arg., cited by Pax & Hoffmann and others as a synonym of *Caryodendron*, was not validly published; hence it is not listed as a synonym.

121. Discoglypremna Prain, Kew Bull. 1911: 317. 1911; Fl. Trop. Afr. 6(1): 931. 1912; Hook. Ic. Pl. 30: t. 2988. 1913; Pax & Hoffm., Pflanzenr. 147. VII (Heft 63): 18. 1914; Keay, Fl. W. Trop. Afr., ed. 2, 1: 403. 1958; Radcliffe-Smith, Fl. E. Trop. Afr. Euphorb. 1: 222. 1987. TYPE: *Discoglypremna caloneura* (Pax) Prain.

A monotypic African genus, distributed from Guinea and São Tome to Cabinda and Uganda. *Discoglypremna* is clearly the African vicariant of *Alchorneopsis*; the two taxa could as easily be regarded as subgenera of a single genus.

122. Alchorneopsis Muell. Arg., Linnaea 34: 156. 1865; DC. Prodr. 15(2): 764. 1866; Fl. Bras. 11(2): 327. 1874; Bentham, Gen. Pl. 3: 315. 1880; Pax & Hoffm., Pflanzenr. 147. VII (Heft 63): 267. 1914; Webster, Ann. Missouri Bot. Gard. 54: 284. 1968. TYPE: *Alchorneopsis floribunda* (Benth.) Muell. Arg.

A neotropical genus of three described species that are probably conspecific, recorded from the West Indies (Puerto Rico), Panama, Brazil, and the Guianas.

Tribe 25. BERNARDIEAE Webster, Taxon 24: 596. 1975. Acalypheae subtribe Mercurialinae series Bernardiiformes Pax & Hoffm., Pflanzenr. 147. VII (Heft 63): 13. 1914. TYPE: *Bernardia* Houstoun ex Miller.

Monoecious or dioecious shrubs or herbs; indumentum simple or stellate; leaves alternate, simple, penninerved, often with laminar glands, stipulate; inflorescences terminal, pseudoterminal, or axillary, racemose or spicate; flowers apetalous. Staminate calyx splitting into 3 or 4 valvate segments; disk intrastaminal, pulviniform, dissected, or obsolete; stamens 3–60, filaments free; anthers muticous or apiculate; pollen grains 3-lobed, 3-colporate, colpi inoperculate, conspicuously marginate, sexine perforate-tectate; pistillode rudimentary or absent. Pistillate sepals 4–6, imbricate; disk annular or dissected; ovary 3-locular; styles bifid, branches sometimes lacerate. Fruit capsular; seeds ecarunculate, smooth, roundish, sometimes carinate.

This tribe includes only part of the genera assigned to the series Bernardiiformes by Pax & Hoffmann (1914). The type genus, *Bernardia*, has often been associated with *Adelia*, and indeed Baillon (1858) treated *Bernardia* as a synonym of *Adelia*. However, the pollen of *Adelia* differs markedly in having operculate colpi and a finely punctate-tectate sexine; tribes Bernardieae and Adelieae do not appear to be closely related. Hutchinson (1969) referred *Bernardia* to tribe Macarangeae, but its pollen is very different from *Macaranga*.

KEY TO THE GENERA OF TRIBE BERNARDIEAE

1a. Styles bifid; stamens 4–50, anther connective not greatly enlarged.
  2a. Leaf blades not stipellate.

3a. Stamens 30 or fewer, anthers emarginate; seeds carinate ____ 123. *Bernardia*
3b. Stamens more than 30, anthers apiculate; seeds not carinate ___ 124. *Necepsia*
2b. Leaf blades stipellate.
4a. Leaves penninerved, short-petioled; anthers apiculate _____ 125. *Paranecepsia*
4b. Leaves palmatinerved, long-petioled; anthers muticous _____ 126. *Discocleidion*
1b. Styles unlobed, dilated, forming a cap over the top of the ovary; stamens 2 or 3, anther connective greatly dilated _____ 127. *Adenophaedra*

123. Bernardia Houstoun ex Miller, Gard. Dict. abr. ed. 1754; Houstoun ex P. Browne, Civ. Nat. Hist. Jamaica 361. 1756; Muell. Arg., Prodr. 15(2): 915. 1866; Fl. Bras. 11(2): 389. 1874; Bentham, Gen. Pl. 3: 308. 1880; Pax & Hoffm., Pflanzenr. 147. VII (Heft 63): 21. 1914; Fawc. & Rend., Fl. Jam. 4: 290. 1920; Pax & Hoffm., Natürl. Pflanzenfam. ed. 2, 19c: 105. 1931; Standley & Steyerm., Fieldiana Bot. 24(6): 52. 1949; Buchheim, Willdenowia 2: 291. 1960; 3: 217. 1962; Allem, Rev. Brasil. Biol. 39: 529. 1979; Liogier, Fl. Española 4: 85. 1986. TYPE: *Bernardia carpinifolia* Griseb.

Bivonia Spreng., Neue Entd. Pflanzenk. 2: 116. 1820. TYPE: *Bivonia axillaris* Spreng. [= *Bernardia axillaris* (Spreng.) Muell. Arg.].

Traganthus Klotzsch, Arch. Naturgesch. 7(1): 188. 1841. TYPE: *Traganthus sidoides* Kl. [= *Bernardia sidoides* (Kl.) Muell. Arg.].

Phaedra Klotzsch ex Endlicher, Gen. Pl. Suppl. 4(3): 88. 1850. TYPE: *Bernardia jacquiniana* Muell. Arg. [lectotype, selected here].

Polyboea Klotzsch ex Endlicher, Gen. Pl. Suppl. 4(3): 88. 1850. TYPE: *Acalypha corensis* Jacq. [= *Bernardia corensis* (Jacq.) Muell. Arg.].

Tyria Klotzsch ex Endlicher, Gen. Pl. Suppl. 4(3): 88. 1850. TYPE: *Bernardia mexicana* (Hook. & Arn.) Muell. Arg. [lectotype, selected here].

Alevia Baillon, Etude Gén. Euphorb. 508. 1858. TYPE: *Alevia leptotaschia* Baillon, sphalm. [= *Bernardia interrupta* (Schlecht.) Muell. Arg.].

Passaea Baillon, Etude Gén. Euphorb. 507. 1858. TYPE: *Passaea spartioides* Baillon [= *Bernardia spartioides* (Baill.) Muell. Arg.].

A diverse American genus of ca. 50 species, divided into seven sections by Pax & Hoffmann (1914, 1931); some of these, especially section *Traganthus*, may deserve generic status on further study.

124. Necepsia Prain, Kew Bull. Misc. Inf. 1910: 343. 1910; Hook. Ic. Pl. 30: t. 2987. 1913; Pax & Hoffm., Pflanzenr. 147. VII (Heft 63): 16. 1914; Bouchat & Léonard, Bull. Jard. Bot. Brux. 56: 179. 1986; Radcliffe-Smith, Fl. E. Trop. Afr. Euphorb. 1: 218. 1987. TYPE: *Necepsia afzelii* Prain.

Neopalissya Pax, in Pax & Hoffm., Pflanzenr. 147. VII (Heft 63): 16. 1914. *Palissya* Baillon, Etude Gén. Euphorb. 502. 1858 (non *Palissya* Endlicher, 1847). TYPE: *Neopalissya castaneifolia* (Baillon) Pax [= *Necepsia castaneifolia* (Baillon) Bouch. & Léon.].

As interpreted by Bouchat & Léonard (1986), *Necepsia* is an African genus of three species.

125. Paranecepsia Radcliffe-Smith, Kew Bull. 30: 684. 1976; Fl. E. Trop. Afr. Euphorb. 1: 220. 1987. TYPE: *Paranecepsia alchorneifolia* Radcl.-Sm.

A monotypic east African genus (Tanzania and Mozambique).

126. Discocleidion (Muell. Arg.) Pax & Hoffmann, Pflanzenr. 147. VII (Heft 63): 45. 1914. TYPE: *Discocleidion ulmifolium* (Muell. Arg.) Pax & Hoffm.

A genus of two species found in southeast China and the Ryukyus; reduced to *Alchornea* by Hurusawa (1954).

127. Adenophaedra (Muell. Arg.) Muell. Arg., Fl. Bras. 11(2): 385. 1874; Bentham, Gen. Pl. 3: 314. 1880; Pax & Hoffmann, Pflanzenr. 147. VII (Heft 63): 261. 1914; Croizat, Trop. Woods 88: 30. 1946; Jablonski, Mem. New York Bot. Gard. 17: 140. 1967; Huft, Ann. Missouri Bot. Gard. 75: 1099. 1988. TYPE: *Adenophaedra grandifolia* (Kl.) Muell. Arg. [lectotype, designated by Jablonski, 1967].

A neotropical genus of three species extending from Costa Rica south to Brazil. The relationships of the genus require further study, as it is somewhat aberrant in the tribe Bernardieae. Although Mueller (1866) originally treated *Adenophaedra* as a section of *Bernardia*, Bentham (1880) placed it next to *Caryodendron*, as did Pax & Hoffmann (1914). There is indeed some resemblance, but the pollen studies of Punt (1962) appear to confirm the intuition of Mueller that the closer relationship of *Adenophaedra* is with *Bernardia*.

Tribe 26. PYCNOCOMEAE Hutchinson, Amer. J. Bot. 56: 753. 1969; Webster, Taxon 24: 596. 1975. TYPE: *Pycnocoma* Bentham.

Dioecious trees; indumentum simple, often glandular, or absent; leaves alternate, opposite, or ver-

ticillate, simple, penninerved, eglandular, sometimes resinous; stipules caducous or absent; inflorescences axillary, racemose or paniculate, or contracted into capitula; flowers apetalous. Staminate calyx closed in bud, splitting into 3 or 4 valvate segments; disk glabrous and receptacular, or absent; stamens 15–many, free, anthers sometimes with enlarged connective; pollen grains oblate or subglobose, 3-colporate, colpi short and narrow, inoperculate, sexine tectate-perforate, gemmate or spinulose; pistillode absent. Pistillate sepals 3–7, imbricate; disk glabrous or absent; ovary (2-)3-locular; styles bifid or unlobed. Fruit capsular, often thick-walled and subdrupaceous; seeds ecaruncu-late, testa dry or fleshy.

As defined by Webster (1975) and here, only the type genus *Pycnocoma*, of the genera included by Hutchinson, is retained in the tribe Pycnocomeae; the other genera are relegated to tribes Epiprineae and Plukenetieae. However, the membership of the taxa here included in the Pycnocomeae is still a matter of doubt. The two subtribes recognized here are divergent both morphologically and in geographical distribution, so that they may have to be separated on further study. However, there is some resemblance in pollen characters between *Pycnocoma* and *Blumeodendron*, so the two subtribes are kept together provisionally.

KEY TO THE SUBTRIBES OF TRIBE PYCNOCOMEAE

1a. Monoecious; seed-coat not fleshy; pollen sexine gemmate ..... 26a. Pycnocominae
1b. Dioecious; seed-coat fleshy; pollen sexine punctate-tectate or coarsely reticulate ..... 26b. Blumeodendrinae

Subtribe 26a. PYCNOCOMINAE Webster, subtr. nov. TYPE: *Pycnocoma* Bentham.

Monoicae; stamina numerosa; antherarum connectivum incrassatum; pollinis grana 3-colpoidorata, sexino gemmato; semina non carnosa.

Monoecious shrubs or small trees; leaves alternate or pseudo-verticillate; stamens 50 or more; pistillate flowers sessile; pistillate disk absent; styles elongated, connate below, barely lobed at tip; fruit thin-walled, horned or not; seeds with dry testa.

This subtribe includes three genera, two African and one Malagasian.

KEY TO THE GENERA OF SUBTRIBE PYCNOCOMINAE

1a. Pistillate flower terminating the inflorescence; pistillate disk absent.
2a. Ovary 6-horned, pubescent; staminate flowers distinctly pedicellate; filaments inflexed in bud ..... 128. *Pycnocoma*
2b. Ovary unappendaged, glabrous; staminate flowers subsessile, filaments not inflexed in bud ..... 129. *Droceloncia*
1b. Pistillate flower not terminating inflorescence; pistillate disk annular ..... 130. *Argomuellera*

128. Pycnocoma Bentham, Niger Fl. 508. 1849; Muell. Arg., DC. Prodr. 15(2): 951. 1866; Bentham, Gen. Pl. 3: 326. 1880; Prain, Fl. Trop. Afr. 6(1): 955. 1913; Pax & Hoffm., Pflanzenr. 147. VII (Heft 63): 52. 1914; Leandri, Notul. Syst. (Paris) 9: 161. 1941; Keay, Fl. W. Trop. Afr. ed. 2, 1: 405. 1958; Léonard, Bull. Soc. Roy. Bot. Belge 91: 273. 1959; Racliffe-Smith, Fl. E. Trop. Afr. Euphorb. 1: 228. 1987. TYPE: *Pycnocoma macrophylla* Benth.

A tropical African genus of ca. 15 species.

129. Droceloncia Léonard, Bull. Soc. Roy. Bot. Belge 91: 279. 1959. TYPE: *Droceloncia rigidifolia* (Baillon) Léonard.

A monotypic genus of the Comores and Madagascar.

130. Argomuellera Pax, Bot. Jahrb. 19: 90. 1894; Prain, Fl. Trop. Afr. 6(1): 925. 1912; Leandri, Notul. Syst. (Paris) 9: 161. 1941; Léonard, Bull. Soc. Roy. Bot. Belge 91: 274. 1959; Radcliffe-Smith, Fl. E. Trop. Afr. Euphorb. 1: 225. 1987. *Pycnocoma* sect. *Wetriaria* Muell. Arg., DC. Prodr. 15(2): 952. 1866. *Wetriaria* (Muell. Arg.) Pax, Pflanzenr. 147. VII (Heft 63): 49. 1914. TYPE: *Argomuellera macrophylla* Pax.

An Afro-Malagasian genus of ca. ten species, as delimited by Léonard (1959).

Subtribe 26b. BLUMEODENDRINAE Webster, Taxon 24: 596. 1975. TYPE: *Blumeodendron* (Muell. Arg.) Kurz.

Dioecious trees; leaves long-petiolate, entire, with scalariform veinlets; inflorescences racemose or paniculate; stamens 15–many; anther connective enlarged; pollen grains perforate-tectate or coarsely reticulate; ovary (2-)3-locular; styles unlobed; fruit large, thick-walled; seeds with fleshy testa.

This subtribe includes three Asian genera that differ in aspect from the Pycnocominae by the long-petiolate leaves and more or less paniculate inflorescence.

KEY TO THE GENERA OF SUBTRIBE BLUMEODENDRINAE

1a. Anther connective no more than moderately enlarged, not umbraculiform; pistillate disk tenuous or absent; styles elongated.
  2a. Anther-cells 2; fruit lacking spines or ridges.
    3a. Anther-cells adnate to connective; pistillate disk annular; flowers without glandular hairs ..... 131. *Blumeodendron*
    3b. Anther-cells pendulous; pistillate disk absent; flowers with stalked glandular hairs ..... 132. *Podadenia*
  2b. Anther-cells 4; fruit with spines or ridges ..... 133. *Ptychopyxis*
1b. Anther connective umbraculiform, with 4 pendent locules; pistillate disk massive, pulviniform; styles stigmatiform ..... 134. *Botryophora*

131. Blumeodendron (Muell. Arg.) Kurz, J. Asiatic Soc. Bengal 42: 245. 1873; J. J. Smith, Meded. Depart. Landbouw 10: 458. 1910; Pax & Hoffm., Pflanzenr. 147. VII (Heft 63): 47. 1914; Airy Shaw, Kew Bull. 16: 348. 1963; Whitmore, Tree Fl. Malaya 2: 68. 1973; Airy Shaw, Kew Bull. Add. Ser. 4: 57. 1975; Kew Bull. Add. Ser. 8: 37. 1980; Kew Bull. 36: 267. 1981. TYPE: *Blumeodendron tokbrai* (Bl.) Kurz [lectotype, designated by Wheeler, 1975].

An Asian genus of six species distributed from the Andaman Islands and Burma through Indonesia to the Bismarck Archipelago.

132. Podadenia Thwaites, Enum. Pl. Zey 4: 273. 1861; Muell. Arg., DC. Prodr. 15(2): 791. 1866; Bentham, Gen. Pl. 3: 318. 1880; Hook. f., Fl. Brit. Ind. 5: 422. 1887; Trimen, Handb. Fl. Ceylon 4: 62. 1898; Pax & Hoffm., Pflanzenr. 147. VII (Heft 63): 19. 1914. TYPE: *Podadenia sapida* Thwaites.

A monotypic genus endemic to Sri Lanka. Although combined by Croizat (1942) with *Ptychopyxis*, it is a very distinctive group, as noted by Airy Shaw (1963). Until its status can be critically evaluated, it seems best to retain it as a distinct genus.

133. Ptychopyxis Miquel, Fl. Ned. Ind. Suppl. 402. 1861; Hooker f., Hook. Ic. Pl. 18: t. 1703. 1887; Croizat, J. Arnold Arbor. 23: 47. 1942; Airy Shaw, Kew Bull. 14: 363. 1960; 16: 347. 1963; Whitmore, Tree Fl. Malaya 2: 126. 1973; Airy Shaw, Kew Bull. Add. Ser. 4: 188. 1975; Add. Ser. 8: 197. 1980; Kew Bull. 36: 340. 1981. TYPE: *Ptychopyxis costata* Miq.

Clarorivinia Pax & Hoffm., Pflanzenr. 147. VII (Heft 63): 17. 1914. TYPE: *Clarorivinia chrysantha* (K. Schum.) Pax & Hoffm. [= *Ptychopyxis chrysantha* (K. Schum.) Airy Shaw].

A tropical Asian genus of 10–12 species distributed from Thailand through Indonesia to the Philippines and New Guinea.

134. Botryophora Hooker f., Fl. Brit. Ind. 5: 476. 1888 (nom. cons.); Pax & Hoffm., Natürl. Pflanzenfam. ed. 2, 19c: 228. 1931; Airy Shaw, Kew Bull. 3: 484. 1949; 14: 374. 1960; Hook. Ic. Pl. 36: t. 3576. 1962; Kew Bull. Add. Ser. 4: 61. 1975; Kew Bull. 36: 267. 1981. TYPE: *Botryophora kingii* Hook. f. [= *Botryophora geniculata* (Miq.) Beumée ex Airy Shaw].

A monotypic genus of tropical Asia (Burma to Sumatra and Borneo).

Tribe 27. EPIPRINEAE (Muell. Arg.) Hurusawa, J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 6: 309. 1954. Acalypheae subtribe Epiprineae Muell. Arg., Linnaea 34: 144. 1865; DC. Prodr. 15(2): 1024. 1866. TYPE: *Epiprinus* Griffith.

Monoecious trees or shrubs; indumentum stellate; leaves alternate, simple, pinnately veined, eglandular or with petiolar glands, stipulate; inflorescences terminal or axillary, paniculate, racemose, or spicate (or staminate capitular); flowers apetalous. Staminate calyx closed in bud, splitting into 2–6 valvate segments; disk absent; stamens 5–15, filaments free or connate, usually inflexed in bud (except in *Koilodepas*); pollen grains subglobose to subprolate, 3-colporate, angulaperturate, colpi inoperculate, scarcely marginate, sexine perforate-tectate or rather coarsely reticulate. Pistillate sepals 4–8, imbricate, sometimes foliaceous or toothed; disk absent or rudimentary; ovary 3-(4-) locular; styles free or connate, bifid or multifid. Fruit capsular (rarely drupaceous); seeds subglobose, smooth, dry, ecarunculate.

This tribe includes nine paleotropical genera that have never all been associated in previous treatments, although a number were brought together under subtribe Cephalocrotoninae by Mueller (1866), and by Pax & Hoffmann (1914, 1931) in their series Cladogyniformes. There is considerable resemblance between the Epiprineae and the Agrostistachydeae, and in some respects with the Erismantheae.

KEY TO THE SUBTRIBES OF TRIBE EPIPRINEAE

1a. Staminate calyx splitting into distinct segments; pollen sexine not spinulose; pistillate sepals often persistent, accrescent ..... 27a. Epiprininae
1b. Staminate calyx turbinate, 2–5-lobed, lobes verrucose; pollen sexine spinulose; pistillate sepals caducous ..... 27b. Cephalomappinae

Subtribe 27a. EPIPRININAE Muell. Arg., Linnaea 34: 144. 1865. TYPE: *Epiprinus* Griffith.

Acalypheae subtribe Cephalocrotoneae Muell. Arg., Linnaea 34: 143. 1865. TYPE: *Cephalocroton* Hochst.

Acalypheae subtribe Mercurialinae series Cladogyniformes Pax & Hoffm., Pflanzenr. 147. VII (Heft 63): 264. 1914. TYPE: *Cladogynos* Zipp. ex Span.

Epiprineae subtribe Cleidiocarpinae Thin, Tap Chi Sinh Hoc 10(2): 32. 1988. TYPE: *Cleidocarpon* Airy Shaw.

Leaves entire or dentate, pinnately or palmately veined; staminate flowers in clusters on spicate or racemose axes, or in capitula; pistillate flowers at same nodes as staminate, or proximal; stamens 4–10, filaments free; pollen grains globose, with relatively large colpi, sexine not spinulose; pistillate sepals 4–6, ± persistent; capsule smooth.

The eight genera of this subtribe occur in Africa, Madagascar, and tropical Asia. Although Pax & Hoffmann (1919, 1931) and Hurusawa (1954) maintained *Epiprinus* in a monotypic tribe or subtribe, its relationship to the other genera of Epiprineae enumerated below seems clear from resemblances in pollen and floral structures (e.g., staminate flowers with filaments inflexed in the bud).

KEY TO THE GENERA OF SUBTRIBE EPIPRINAE

1a. Staminate flowers in racemes or spikes; stipules (if present) glandular.
  2a. Pistillate calyx foliose, accrescent, involucrate with deciduous biglandular bracts; styles connate into a column, distally bifid or multifid; stamens 5–15; leaves with petiolar glands ..... 135. *Epiprinus*
  2b. Pistillate calyx neither accrescent nor involucrate; styles ± free, distally multifid; stamens 3 6.
    3a. Filaments inflexed in bud.
      4a. Fruits capsular; leaves eglandular.
        5a. Pistillate sepals entire; staminate flowers not in heads ..... 136. *Symphyllia*
        5b. Pistillate sepals glandular-dissected; staminate flowers in heads ..... 137. *Adenochlaena*
      4b. Fruit indehiscent; petiole biglandular ..... 138. *Cleidiocarpon*
    3b. Filaments not inflexed in bud ..... 139. *Koilodepas*
1b. Staminate flowers in pedunculate capitula; stipules not glandular.
  5a. Inflorescences axillary, inconspicuous; stamens 3 5; pistillate sepals accrescent, unlobed; leaves white-tomentose beneath ..... 140. *Cladogynos*
  5b. Inflorescences terminal; leaves not white-tomentose beneath.
    6a. Pistillate sepals entire, connate; styles free; leaves coriaceous ..... 141. *Cephalocrotonopsis*
    6b. Pistillate sepals pinnatifid; styles connate; leaves thinner ..... 142. *Cephalocroton*

135. Epiprinus Griffith, Notul. Pl. Asiat. 4: 487. 1854; Muell. Arg., DC. Prodr. 15(2): 1024. 1866; Bentham, Gen. Pl. 3: 325. 1880; Hook. f., Fl. Brit. Ind. 5: 463. 1887; Pax & Hoffmann, Pflanzenr. 147. X (Heft 68): 109. 1919; Gagnepain, Bull. Soc. Bot. France 72: 465. 1925; Fl. Indochine 5: 474. 1926; Croizat, J. Arnold Arbor. 23: 52. 1942; Airy Shaw, Kew Bull. 16: 356. 1963; Kew Bull. 26: 259. 1972; Whitmore, Tree Fl. Malaya 2: 95. 1973; Thin, Tap Chi Sinh Hoc 10(2): 30. 1988. TYPE: *Epiprinus malayanus* Griff.

A rather variable genus of ca. six species in tropical Asia, from Assam to Malaya. Mueller (1866), followed by Pax & Hoffmann (1919), placed *Epiprinus* by itself in subtribe Epiprininae, on the basis that the pistillate flower is involucrate.

136. Symphyllia Baillon, Etude Gén. Euphorb. 473. 1858; Muell. Arg., DC. Prodr. 15(2): 763. 1866; Gagnepain, Fl. Indochine 5: 477. 1926. TYPE: *Symphyllia siletiana* Baillon.

A genus of three species distributed from India to Hainan and Malaya. Croizat (1942) combined *Symphyllia* with *Epiprinus* on the basis that *Epiprinus balansae* (Pax & Hoffm.) Gagnep. represents a transitional link between the two taxa. Airy Shaw (1963, 1972) and Thin (1988) followed him in this, but neither discussed the morphology of the pistillate flower or demonstrated that the "involucre" described by Mueller is without systematic significance. It is possible that Croizat was correct, but until the problem is given further study, it seems preferable to maintain *Symphyllia* as distinct.

137. Adenochlaena Baillon, Etude Gén. Euphorb. 472. 1858; Pax, Pflanzenr. 147. II (Heft 44): 12. 1910; Pax & Hoffm., Natürl.

Pflanzenfam. ed. 2, 19c: 124. 1931. TYPE: *Adenochlaena leucocephala* Baillon.

Centrostylis Baillon, Etude Gén. Euphorb. 469. 1858. TYPE: *Centrostylis zeylanica* Baillon [= *Adenochlaena zeylanica* (Baillon) Thw.].

Niedenzua Pax, Bot. Jahrb. 19: 106. 1894. TYPE: *Niedenzua cordata* Pax [= *Adenochlaena leucocephala* Baillon].

A genus of two disjunct species (Madagascar/Comores; Sri Lanka); treated by Mueller (1866) as a section of *Cephalocroton*.

138. Cleidiocarpon Airy Shaw, Kew Bull. 19: 313. 1965; Kew Bull. 32: 410. 1978; Thin, Tap Chi Sinh Hoc 10(2): 32. 1988. TYPE: *Cleidiocarpon laurinum* Airy Shaw.

Sinopimelodendron Tsiang, Acta Bot. Sinica 15: 132. 1973. TYPE: *Sinopimelodendron kwangsiense* Tsiang [= *Cleidiocarpon cavaleriei* (Levl.) Airy Shaw].

A genus of two closely related species of Burma and China; Thin (1988) placed it in a separate subtribe, Cleidiocarpinae.

139. Koilodepas Hasskarl, Versl. Med. Afd. Natuurk. Kon. Akad. Wetensch. 4: 139. 1856; Flora 40: 531. 1857 (as *Coelodepas*); Muell. Arg., DC. Prodr. 15(2): 759. 1866; Bentham, Hook. Ic. Pl. 13: t. 1288. 1879; Gen. Pl. 3: 313. 1880; Hook. f., Fl. Brit. Ind. 5: 419. 1887; Pax, Pflanzenr. 147. VII (Heft 63): 268. 1914; Croizat, J. Arnold Arbor. 23: 50. 1942; Airy Shaw, Kew Bull. 14: 382. 1960; 16: 354. 1963; 26: 284. 1972; Whitmore, Tree Fl. Malaya 2: 103. 1973; Airy Shaw, Kew Bull. Add. Ser. 4: 137. 1975; Airy Shaw, Kew Bull. 36: 310. 1981. TYPE: *Koilodepas bantamense* Hassk.

Calpigyne Blume, Ann. Mus. Bot. Lugd.-Batav. 2: 193. 1857. TYPE: *Calpigyne frutescens* Bl. [= *Koilodepas frutescens* (Bl.) Airy Shaw].

Nephrostylus Gagnepain, Bull. Soc. Bot. France 72: 467. 1925. TYPE: *Nephrostylus poilanei* Gagnep. [= *Koilodepas longifolium* Hook. f.].

A genus of ten species of India and southeastern Asia as far as Hainan and Borneo.

140. Cladogynos Zippelius ex Spanoghe, Linnaea 15: 349. 1841; Muell. Arg., DC. Prodr. 15(2): 895. 1866; Bentham, Gen. Pl. 3: 323. 1880; J. J. Smith, Meded. Dept. Landb. 10: 383. 1910; Pax, Pflanzenr. 147. VII (Heft 63): 264. 1914; Gagnepain, Fl. Indochine 5: 478. 1926; Backer & Bakhuizen, Fl. Java 1: 485. 1963; Airy Shaw, Kew Bull. 26: 232. 1972. TYPE: *Cladogynos orientalis* Zipp. ex Span.

Adenogynum Reichenbach & Zollinger, Acta Soc. Regiae Sci. Indo-Neerl. 1: 23. 1856. TYPE: *Adenogynum discolor* Reich. & Zoll. [= *Cladogynos orientalis* Zipp. ex Span.].

A monotypic genus of tropical southeast Asia, Thailand to the Philippines, Java, and Timor.

141. Cephalocrotonopsis Pax, Pflanzenr. 147. II (Heft 44): 15. 1910; Radcliffe-Smith, Kew Bull. 28: 131. 1973. TYPE: *Cephalocrotonopsis socotrana* (Balf. f.) Pax.

A monotypic genus of Socotra; reduced by Radcliffe-Smith (1973) to a section of *Cephalocroton*.

142. Cephalocroton Hochstetter, Flora 24: 370. 1841; Muell. Arg., DC. Prodr. 15(2): 760. 1866; Bentham, Gen. Pl. 3: 307. 1880; Pax, Pflanzenr. 147. II (Heft 44): 7. 1910; Prain, Fl. Trop. Afr. 6(1): 843. 1912; Radcliffe-Smith, Kew Bull. 28: 123. 1973; Fl. E. Trop. Afr. Euphorb. 1: 282. 1987. TYPE: *Cephalocroton cordofanus* Hochst.

An Old World genus of five species recorded from east Africa, Madagascar and the Comores, and Sri Lanka.

Subtribe 27b. CEPHALOMAPPINAE Webster, Taxon 24: 597. 1975. TYPE: *Cephalomappa* Baillon.

Leaves entire, pinnately veined; staminate flowers in capitula on racemose axes, pistillate flowers at proximal nodes of inflorescence; stamens 2–4, filaments connate; pollen grains globose, coarsely reticulate, reticulum spinulose; pistillate sepals 4–6, deciduous; capsule verrucose.

This subtribe includes only the type genus.

143. Cephalomappa Baillon, Adansonia I. 11: 130. 1874; Bentham, Gen. Pl. 3: 323. 1880; Pax, Pflanzenr. 147. II (Heft 44): 16. 1910; Airy Shaw, Kew Bull. 14: 378. 1960; Kostermans, Reinwardtia 5: 413. 1961; Airy Shaw, Kew Bull. Add. Ser. 4: 66. 1975; Kew Bull. 36: 274. 1981. TYPE: *Cephalomappa beccariana* Baillon.

Muricococcum Chun & How, Acta Phytotax. Sin. 5: 14. 1956. TYPE: *Muricococcum sinense* Chun & How [= *Cephalomappa sinensis* (Chun & How) Kosterm.].

A genus of five species in southeast Asia (Malaya to Sumatra and Borneo, southern China).

Tribe 28. ADELIEAE Webster, Taxon 24: 597. 1975. Acalypheae subtribe Mercurialinae series Adeliiformes Pax & Hoffm., Pflanzenr. 147. VII (Heft 63): 59. 1919. TYPE: *Adelia* L.

Dioecious (rarely monoecious) trees or shrubs; indumentum simple or stellate; leaves alternate, simple, entire or dentate, eglandular; stipules small; inflorescences axillary, flowers apetalous, in glomerules or racemes. Staminate calyx splitting into 4 or 5 valvate segments; disk extrastaminal, annular or obsolete; stamens 8–18, ± connate at base; anthers versatile; pollen grains 3-(4-)colporate, colpi operculate, exine tectate-perforate with polygonally arranged nanospinules; pistillode present or absent. Pistillate sepals 5 or 6, valvate or open at anthesis, often reflexed; disk annular, glabrous or pubescent; seeds roundish, smooth, ecarunculate (rarely carunculate).

An American tribe of five genera.

KEY TO THE GENERA OF TRIBE ADELIEAE

1a. Indumentum simple; stipules deciduous; pollen grains with finely perforate tectum; styles lacerate.
  2a. Ovary 3-locular; staminate disk present; stamens 8–20; seeds ecarunculate.
    3a. Pistillode present; staminate disk annular or segmented; flowers in axillary clusters ..... 144. *Adelia*
    3b. Pistillode absent; staminate disk of interstaminal processes; flowers in racemes ..... 145. *Crotonogynopsis*
  2b. Ovary 2-locular; staminate disk absent; stamens more than 20; seeds carunculate ..... 146. *Enriquebeltrania*
1b. Indumentum stellate or stellate-lepidote; stipules absent; pollen grains with coarsely perforate tectum.
  4a. Pistillate disk entire; styles bifid or subentire; filaments free; pollen 3-colporate; leaves triplinerved, indumentum stellate ..... 147. *Lasiocroton*
  4b. Pistillate disk lobed; styles lacerate; filaments ± connate; pollen 4-colporate; leaves penninerved, indumentum stellate-lepidote ..... 148. *Leucocroton*

144. Adelia L., Syst. Nat. ed. 10, 2: 1298. 1759 (nom. cons.); Bentham, Gen. Pl. 3: 312. 1880; Pax, Pflanzenr. 147. VII (Heft 63): 64. 1914; Fawc. & Rend., Fl. Jam. 4: 291. 1920; Webster, Ann. Missouri Bot. Gard. 54: 272. 1968; Sneep & De Roon, Fl. Neth. Ant. 3: 254. 1984. TYPE: *Adelia ricinella* L. (typ. cons.).

Ricinella Muell. Arg., Linnaea 34: 153. 1865. TYPE: *Ricinella pedunculosa* (A. Rich.) Muell. Arg. [= *Adelia ricinella* L.].

A neotropical genus of ca. 10–12 species, Mexico to Paraguay and Brazil but best represented in the West Indies.

145. Crotonogynopsis Pax, Bot. Jahrb. 26: 328. 1899; Prain, Fl. Trop. Afr. 6(1): 924. 1912; Pax & Hoffmann, Pflanzenr. 14. XII (Heft 63): 14. 1914; Keay, Fl. W. Trop. Afr. ed. 2, 1: 404. 1958; Radcliffe-Smith, Fl. Trop. E. Afr. Euphorb. 1: 213. 1987. TYPE: *Crotonogynopsis usambarica* Pax.

A monotypic African genus (Zaire to Uganda and Tanzania).

146. Enriquebeltrania Rzedowski, Bol. Soc. Bot. México 38: 75. 1979. *Beltrania* Miranda, Bol. Soc. Bot. México 21: 4. 1957 (non *Beltrania* Penzig, 1882). TYPE: *Enriquebeltrania crenatifolia* (Miranda) Rzedowski [*Beltrania crenatifolia* Miranda].

A monotypic genus of the Yucatan peninsula, very similar to *Adelia* and questionably distinct.

147. Lasiocroton Grisebach, Fl. Brit. W. Ind. 46. 1859; Abh. Königl. Ges. Wiss. Göttingen 9: 20. 1861; Bentham, Gen. Pl. 3: 317. 1880; Pax, Pflanzenr. 147. VII (Heft 63): 60. 1914; Fawc. & Rend., Fl. Jam. 4: 293. 1920; Alain, Fl. Cuba 3: 87. 1953. TYPE: *Lasiocroton macrophyllus* (Sw.) Griseb.

A West Indian genus of five species (Bahamas, Cuba, Jamaica, and Hispaniola).

148. Leucocroton Grisebach, Abh. Königl. Ges. Wiss. Göttingen 9: 20. 1861; Muell. Arg., DC. Prodr. 15(2): 757. 1866; Bentham. Gen. Pl. 3: 312. 1880; Pax, Pflanzenr. 147. VII (Heft 63): 62. 1914; Urban, Ber. Deutsch. Bot. Ges. 36: 504. 1918; Alain, Fl. Cuba 3: 89. 1953; Borhidi, Acta Bot. Acad. Sci. Hungar. 21: 222. 1975. TYPE: *Leucocroton wrightii* Griseb.

A genus of 20 species of Cuba and Hispaniola.

Tribe 29. ALCHORNEAE (Hurusawa) Hutchinson, Amer. J. Bot. 56: 752. 1969. Acalypheae subtribe Alchorneinae Hurus., J. Fac. Sci. Univ. Tokyo III. 6: 302. 1954. TYPE: *Alchornea* Sw.

Dioecious trees or shrubs; indumentum simple or stellate; leaves alternate, entire or dentate, pinnately or palmately veined, sometimes stipellate or with laminar glands; stipules mostly deciduous.

sometimes obsolete; inflorescences terminal or axillary, spicate or paniculate (compounded spikes); bracts glandular or eglandular; flowers apetalous. Staminate calyx splitting into 2–5 valvate segments; disk intrastaminal or absent; stamens (2–) 4–60, free; anthers introrse, muticous or apiculate; pollen grains 3-colporate, colpi operculate, sexine rugulose to vermiculate; pistillode rudimentary or absent. Pistillate sepals 3–8, imbricate, usually persistent, sometimes glandular; disk mostly rudimentary or absent; ovary 2- or 3- (rarely 4-)locular; styles entire to bifid or multifid. Fruit capsular; seeds smooth or tuberculate, testa not fleshy.

As delimited earlier (Webster, 1975) and here, tribe Alchorneae is somewhat more comprehensive than the circumscription of Hutchinson (1969), since *Conceveiba* and its allies—referred to the Malloteae by Hutchinson—are included. The distinctive pollen grains that characterize this tribe indicate an affinity to *Mallotus* and related genera, but are distinctive in the operculate colpi.

KEY TO THE SUBTRIBES OF TRIBE ALCHORNEAE

1a. Styles entire or if distinctly bifid, then indumentum simple; stamens 4–9; staminate inflorescences axillary ..... 29a. ALCHORNEINAE
1b. Styles bifid; indumentum stellate; stamens 15–60; staminate inflorescences terminal or axillary ..... 29b. CONCEVEIBINAE

Subtribe 29a. ALCHORNEINAE Hurusawa, J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 6: 302. 1954. Acalypheae subtribe Mercurialinae series Alchorneiformes Pax & Hoffm., Pflanzenr. 147. VII (Heft 63): 220. 1914. TYPE: *Alchornea* Sw.

Indumentum simple or stellate; staminate inflorescences axillary; stamens 2–9; pistillate sepals eglandular; styles mostly entire, often stigmatiform or dilated; ovary 2- or 3-(rarely 4-)locular.

This subtribe of six genera with ca. 70 species is well represented in both the Neotropics and Paleotropics. Most of the genera are only weakly separated from *Alchornea*, and the number may be reduced on further study.

KEY TO THE GENERA OF SUBTRIBE ALCHORNEINAE

1a. Styles bifid; indumentum simple.
2a. Dioecious; ovary smooth; pistillode absent; seeds ecarunculate ..... 149. *Orfilea*
2b. Monoecious; ovary cristate; pistillode present; seeds carunculate ..... 150. *Bossera*
1b. Styles unlobed or bifid only at tip.
3a. Styles elongated and slender; indumentum simple or stellate; ovary 2- or 3-locular ..... 151. *Alchornea*
3b. Styles stigmatiform or dilated; indumentum simple; ovary 3-locular.
4a. Stamens usually 8, free; stigmas smooth; pistillate sepals glandular at base ..... 152. *Coelebogyne*
4b. Stamens 2–4, basally connate.
5a. Stamens 4; styles elongated, dilated; seeds ecarunculate ..... 153. *Aparisthmium*
5b. Stamens 2 or 3; styles stigmatiform; seeds minutely carunculate ..... 154. *Bocquillonia*

149. Orfilea Baillon, Etude Gén. Euphorb. 452. 1858. TYPE: *Orfilea coriacea* Baillon.

Diderotia Baillon, Adansonia I. 1: 274. 1861. *Laurembergia* Baillon, Etude Gén. Euphorb. 451. 1858 (sphalm. *Lautembergia*; non *Laurembergia* Bergius, 1767). TYPE: *Diderotia multispicata* (Baillon) Baillon [= **Orfilea multispicata** (Baillon) Webster, comb. nov.].

A Malagasian genus of four species, closely related to *Alchornea* but differing in the distinctly bifid styles. A species from Mauritius discussed by Coode (Kew Bull. 33: 111. 1978) also appears to belong to this genus: **Orfilea neraudiana** (Baillon) Webster (comb. nov.; based on *Claoxylon neraudianum* Baillon, Adansonia I. 1: 280. 1861).

150. Bossera Leandri, Adansonia II. 2: 216. 1962. TYPE: *Bossera cristatocarpa* Leandri.

This monotypic genus described from Madagascar is very close to *Alchornea* and is weakly distinguished by its androecium of ten stamens and the distinctively cristate ovary.

151. Alchornea Swartz, Prodr. 6, 98. 1788; Fl. Ind. Occ. 2: 1153. 1800; Muell. Arg., DC. Prodr. 15(2): 899. 1866; Fl. Bras. 11(2): 374. 1874; Bentham, Gen. Pl. 3: 314. 1880; Pax, Pflanzenr. 147. VII (Heft 63): 220. 1914; Webster, Ann. Missouri Bot. Gard. 54: 279. 1968; 75: 1100. 1989; Whitmore, Tree Fl. Malaya 2: 53. 1973; Dyer, Gen. S. Afr. Fl. Pl. ed. 3, 317. 1975; Airy Shaw, Kew Bull. Add. Ser. 4: 28. 1975; Thin, Tap Chi Sinh Hoc 6(3): 26. 1984. TYPE: *Alchornea latifolia* Sw.

Cladodes Loureiro, Fl. Cochinch. 574. 1790. TYPE: *Cladodes rugosa* Lour. [= *Alchornea rugosa* (Lour.) Muell. Arg.].

Hermesia Humb. & Bonpl. ex Willd., Sp. Pl. 4: 809. 1805. TYPE: *Hermesia castanifolia* Humb. & Bonpl. ex Willd. [= *Alchornea castanifolia* (Humb. & Bonpl. ex Willd.) A. Juss.].

Schousboea Schumacher, Beskr. Guin. Pl. 449. 1827 (non Willd., 1799). TYPE: *Schousboea cordifolia* Schum. [= *Alchornea cordifolia* (Schum.) Muell. Arg.].

Stipellaria Bentham, J. Bot. Kew Gard. Misc. 6: 2. 1854. TYPE: *Stipellaria trewioides* Benth. [= *Alchornea trewioides* (Benth.) Muell. Arg.; lectotype, designated by Thin, 1984].

Lepidoturus Bojer ex Baillon, Etude Gén. Euphorb. 448. 1858. TYPE: *Lepidoturus alnifolius* Boj. ex Baillon [= *Alchornea alnifolia* (Baillon) Pax & Hoffm.].

Bleekeria Miquel, Fl. Ind. Bat. 1(2): 407. 1859 (non Hassk., 1855). TYPE: *Bleekeria zollingeri* (Hassk.) Miq. [= *Alchornea villosa* (Benth.) Muell. Arg.].

A variable genus of ca. 50 species distributed in the tropics of both the New World and Old World. Pax (1914) drew the generic boundaries more narrowly than Mueller (1866) by recognizing such segregates as *Aparisthmium* and *Coelebogyne*. However, the Paxian genus still includes three sections, and the relationships between these and the segregate taxa badly need clarification.

152. Coelebogyne J. Smith, Proc. Linn. Soc. London 1: 41. 1839; Baillon, Etude Gén. Euphorb. 416. 1858; Pax, Pflanzenr. 147. VII (Heft 63): 255. 1914. TYPE: *Coelebogyne ilicifolia* J. Smith.

A monotypic genus from tropical Australia, very weakly distinguished from *Alchornea* and perhaps better treated as a section of that genus.

153. Aparisthmium Endlicher, Gen. Pl. 1112. 1840; nom. cons. prop.; Pax, Pflanzenr. 147. VII (Heft 63): 257. 1914; Jablonski, Mem. New York Bot. Gard. 17: 135. 1967. *Conceveibum* A. Rich. ex A. Jussieu, Euphorb. Tent. 42. 1824. TYPE: *Conceveibum cordatum* A. Juss. [= *Aparisthmium cordatum* (A. Juss.) Baillon).

In the concept of Pax (1914), accepted by Jablonski and other neotropical floristic authors, *Aparisthmium* is a monotypic neotropical genus widely distributed from Colombia to Bolivia and southern Brazil. Unfortunately, the genus is technically a synonym of *Conceveiba*, because Endlicher cited A. Jussieu's figure 42B, which in the legend is clearly indicated as Aublet's *Conceveiba guianensis*. Endlicher's description, on the other hand, clearly seems to fit the plant that Baillon and later writers have accepted as *Aparisthmium*. If Endlicher's citation is regarded as a misprint, then *Aparisthmium* becomes a synonym of *Conceveibum* Rich. ex A. Juss., unless *Conceveibum* can be regarded as an intentional orthographic variant of *Conceveiba*. The easiest course out of this tangle would be to propose the generic name *Aparisthmium* for conservation, which seems warranted in view of the abundance of the plant in neotropical vegetation.

154. Bocquillonia Baillon, Adansonia I. 2: 225. 1861; Muell. Arg., DC. Prodr. 15(2): 894. 1866; Bentham, Gen. Pl. 3: 313. 1880; Pax, Pflanzenr. 147. VII (Heft 63): 260. 1914; Airy Shaw, Kew Bull. 29: 321. 1974; McPherson & Tirel, Fl. Nouv.-Calédonie 14(1): 114. 1987. TYPE: *Bocquillonia sessiliflora* Baillon [designated by McPherson & Tirel, 1987].

Ramelia Baillon, Adansonia I. 11: 132. 1874. TYPE: *Ramelia codonostylis* Baillon [= *Bocquillonia codonostylis* (Baillon) Airy Shaw].

As treated by McPherson & Tirel (1987), *Bocquillonia* is a genus of 14 species endemic to New Caledonia.

Subtribe 29b. CONCEVEIBINAE Webster, Taxon 24: 597. 1975. TYPE: *Conceveiba* Aubl.

Leaves long-petiolate, entire or subentire, not stipellate; indumentum stellate (at least in part); floral disk absent; stamens 15–60; pistillate sepals often glandular; ovary 2–3-locular; styles bifid.

This subtribe of three genera and about ten species was thought to be entirely American until the recent discovery of *Conceveiba* in west Africa. Pax & Hoffmann (1914) included *Conceveiba* and *Gavarretia* in their series Trewiiformes (Malloteae), an entirely paleotropical group.

KEY TO THE GENERA OF SUBTRIBE CONCEVEIBINAE

1a. Inflorescences terminal.
  2a. Pistillate sepals separate, often glandular; anthers muticous; ovary 3-locular; style-branches blunt ..... 155. *Conceveiba*
  2b. Pistillate sepals eglandular, connate, lobes scarcely evident; anthers apiculate; ovary 2-locular; style-branches acute ..... 156. *Gavarretia*
1b. Inflorescences axillary; anthers muticous ..... 157. *Polyandra*

155. Conceveiba Aublet, Hist. Pl. Guiane Fr. 923. 1775; Muell. Arg., DC. Prodr. 15(2): 895. 1866; Bentham, Gen. Pl. 3: 316. 1880; Pax, Pflanzenr. 147. VII (Heft 63): 214. 1914; Jablonski, Mem. New York Bot. Gard. 17: 131. 1967; Thomas, Ann. Missouri Bot. Gard. 77: 856. 1990. TYPE: *Conceveiba guianensis* Aubl.

Conceveibastrum (Muell. Arg.) Pax & Hoffm., Pflanzenr. 147. VII (Heft 63): 217. 1914. TYPE: *Conceveibastrum martianum* (Baillon) Pax & Hoffm. [= *Conceveiba martiana* Baillon].

Veconcibea (Muell. Arg.) Pax & Hoffm., Pflanzenr. 147. VII (Heft 63): 218. 1914. TYPE: *Veconcibea lat-*

folia (Benth.) Pax & Hoffm. [= *Conceveiba latifolia* Benth.].

A genus of seven or eight neotropical species extending from Costa Rica to Amazonian Peru and Brazil, and one recently discovered African species from Gabon (Thomas, 1990).

156. Gavarretia Baillon, Adansonia I. 1: 185, t. 7. 1861; Bentham, Gen. Pl. 3: 316. 1880; Pax, Pflanzenr. 147. VII (Heft 63): 213. 1914; Jablonski, Mem. New York Bot. Gard. 17: 130. 1967. TYPE: *Gavarretia terminalis* Baillon.

A monotypic South American genus; the single species occurs in Amazonian Venezuela, Guiana, and Brazil. Mueller (1874) treated *Gavarretia* as a section of *Conceveiba*, and this may yet prove to be the best systematic disposition.

157. Polyandra Leal, Arch. Jard. Bot. Rio de Janeiro 11: 63. 1951. TYPE: *Polyandra bracteosa* Leal.

A poorly understood genus known only from the type species in the Brazilian Amazon; pistillate flowers and fruits are still unknown.

Tribe 30. ACALYPHEAE Dumortier, Anal. Fam. Pl. 45. 1829. TYPE: *Acalypha* L.

Monoecious or dioecious trees, shrub, or herbs; indumentum simple or stellate; leaves alternate or opposite, simple, entire or dentate, pinnately or palmately nerved, often punctate or with laminar glands, stipulate; inflorescences terminal or axillary, unisexual or bisexual, bracts sometimes glandular; flowers apetalous. Staminate calyx closed in bud, valvately splitting into 2–5 segments; disk receptacular (intrastaminal), of interstaminal processes, or absent; stamens 4–many, usually free; anthers sometimes apiculate, anther-sacs sometimes pendulous; pollen grains globose, brevicolporate or porate, apertures not or scarcely operculate; sexine coarsely foveolate to striate or rugulose; pistillode usually absent. Pistillate sepals mostly 3–6, free; disk cupular or absent; ovary 2–4-locular; styles free or basally connate, unlobed to lacerate. Fruit capsular or drupaceous; seeds carunculate or ecarunculate, testa dry or fleshy.

The largest tribe of Acalyphoideae, here divided into 11 subtribes with 30 genera and over 1000 species.

KEY TO THE SUBTRIBES OF TRIBE ACALYPHEAE

1a. Seeds carunculate; inflorescences terminal; indumentum stellate or absent; styles bifid.
  2a. Monoecious; filaments connate into fascicles; pistillate sepals deciduous; stipules connate ——— 30a. Ricininae
  2b. Dioecious; filaments free; pistillate sepals persistent; stipules free ——— 30b. Adrianinae
1b. Seeds ecarunculate, or if carunculate then inflorescences axillary, or styles unlobed.
  3a. Stamens not connate into fascicles.
    4a. Anther-sacs not vermiform and pendulous; pollen colporate; seeds usually ecarunculate.
      5a. Indumentum usually simple (except Lobaniliinae); leaves alternate, eglandular or with embedded laminar glands, not granulose-glandular.
        6a. Herbs, often with opposite leaves; indumentum simple; styles undivided.
          7a. Staminate sepals free; stamens free; ovary 2-locular; pollen grains 3-colporate; anthers not apiculate; cotyledons broader than radicle ——— 30c. Mercurialinae
          7b. Staminate sepals connate; filaments connate; ovary 3-locular; pollen grains inaperturate; anthers apiculate; cotyledons scarcely broader than radicle ——— 30d. Dysopsidinae
        6b. Shrubs or trees (or herbs with bifid styles).
          8a. Anther-sacs not parted to the connective; staminate disk absent; leaves mostly with laminar glands.
            9a. Styles bifid; anthers 2-locular; pollen grains vermiculate-rugulose; seed-coat dry or fleshy ——— 30e. Cleidiinae
            9b. Styles unlobed; anthers 3–4-locular; pollen grains spinulose-rugulose; seed-coat usually fleshy ——— 30f. Macaranginae
          8b. Anther-sacs parted to the connective, erect or pendulous; interstaminal disk present; styles unlobed.
            10a. Indumentum simple ——— 30g. Claoxylinae
            10b. Indumentum stellate ——— 30h. Lobaniliinae
      5b. Indumentum usually stellate; leaves often opposite, often with embedded laminary glands and usually glandular-granulose as well; usually dioecious; inflorescences often terminal; staminate disk present or absent; pollen grains ± spinulose-rugulose ——— 30i. Rottlerinae
    4b. Anthers vermiform and pendulose; staminate disk absent; pollen porate; styles lacerate; seeds ± carunculate; pistillate bracts usually large and foliaceous ——— 30j. Acalyphinae
  3b. Stamens many, connate into fascicles; shrubs or trees with alternate eglandular leaves, indumentum simple or lepidote ——— 30k. Lasiococcinae

Subtribe 30a. RICININAE Grisebach, Fl. Brit. W. Ind. 37. 1859; Abh. Königl. Ges. Wiss. Göttingen 9: 15. 1860; Muell. Arg., DC. Prodr. 15(2): 143. 1866; Pax & Hoffm., Pflanzenr. 147. XI (Heft 68): 112. 1919; Natürl. Pflanzenfam. ed. 2, 19c: 149. 1931; Webster, Taxon 24: 597. 1975. TYPE: *Ricinus* L.

Monoecious trees or shrubs (herbs in temperate climates); indumentum absent; leaves alternate, long-petiolate, palmately lobed; stipules connate into a sheath, deciduous; inflorescences terminal, paniculate, proximal cymules staminate, distal pistillate; bracts glandular; stamens many, filaments united into branching fascicles; pollen grains 3-colporate, colpi narrow and inoperculate; pistillate flowers pedicellate; ovary muricate; styles bifid; capsule echinate; seeds carunculate.

As here defined, subtribe Ricininae is restricted to the single genus *Ricinus*. Pax & Hoffmann (1919) also included *Homonoia* and *Lasiococca* in the Ricininae, mainly because of their rather similar androecium of stamens united into fascicles. However, *Ricinus* differs from those genera (here referred to subtribe Lasiococcinae) in its terminal inflorescence, distinctly carunculate seeds, palmately lobed leaves with glandular petiole, and bifid styles. I am inclined to agree with Airy Shaw (1974) that the character of fasciculate stamens is homoplasious, and the Ricininae do not appear closely related to the Lasiococcinae. On the other hand, *Adriana* is much more similar to *Ricinus* and appears to be the most closely related genus.

158. Ricinus L., Sp. Pl. 1007. 1753; Gen. Pl. ed. 5, 437. 1754; Muell. Arg., DC. Prodr. 15(2): 1016. 1866; Bentham, Gen. Pl. 3: 321. 1880; Pax & Hoffm., Pflanzenr. 147. XI (Heft 68): 119. 1919; Webster, J. Arnold Arbor. 48: 379. 1967; Correll & Correll, Fl. Bahama Arch. 840. 1982; Radcliffe-Smith, Fl. E. Trop. Afr. Euphorb. 1: 322. 1987. TYPE: *Ricinus communis* L.

A monotypic genus native to northeast Africa (according to Radcliffe-Smith), now widely cultivated and ruderal in tropical and subtropical regions worldwide.

Subtribe 30b. ADRIANINAE Bentham, Gen. Pl. 3: 250. 1880; Webster, Taxon 24: 597. 1975. Tribe Adrianeae (Benth.) Pax, Pflanzenr. 147. II (Heft 44): 1. 1910. TYPE: *Adriana* Gaud.

Dioecious; indumentum stellate or absent; leaves alternate or opposite, unlobed or palmately lobed, stipules glandular; inflorescences spicate, terminal or opposite the leaves, bracts glandular; stamens numerous, free; anthers apiculate, sacs adnate to linear connective; ovary 3-locular, smooth; styles bifid; fruit capsular; seeds carunculate.

In contrast to the concepts of Bentham (1880) and Pax (1910), subtribe Adrianinae is here restricted to the type genus *Adriana*. Pax (1910) rather slavishly followed Bentham in including with in his Adrianinae such unrelated genera as *Manihot* and *Pachystroma*. In his later work (Pax & Hoffmann, 1931), he abandoned the tribe Adrianeae and included *Adriana* in his subtribe Mercurialinae adjacent to *Conceveiba* and *Gavarretia*, which is a better and not implausible suggestion of affinity.

159. Adriana Gaudichaud, Ann. Sci. Nat. Paris 5: 223. 1825; Muell. Arg., DC. Prodr. 15(2): 889. 1866; Bentham, Fl. Austral. 6: 133. 1873; Gen. Pl. 3: 306. 1880; Pax, Pflanzenr. 147. II (Heft 44): 17. 1910; Airy Shaw, Kew Bull. 35: 589. 1980. TYPE: *Adriana tomentosa* Gaud. [lectotype].

A genus endemic to Australia; treated by Airy Shaw (1980) as having five species and several varieties. The resemblances between *Ricinus* and *Adriana* appear too significant to be explained away as due to convergence, despite the great geographical disjunction. However, *Adriana* also has a number of characters in common with genera such as *Cephalocroton* and *Cephalomappa* that were included in the Adrianeae by Pax (1919) but are referred to the Epiprineae here. It is possible, therefore, that *Adriana* provides the phylogenetic link between the tribe Epiprineae and subtribe Ricininae. It may be necessary to remove the Adrianinae and Ricininae from the Acalypheae as we accumulate further knowledge.

Subtribe 30c. MERCURIALINAE Pax, Natürl. Pflanzenfam. ed. 1, 3(5): 46. 1890. Acalypheae subtribe Mercurialinae series Mercurialiiformes Pax & Hoffm., Pflanzenr. 147. VII (Heft 63): 270. 1914. TYPE: *Mercurialis* L.

Monoecious or dioecious herbs; indumentum simple; leaves alternate or opposite, pinnately veined, eglandular; inflorescences axillary, spicate or in glomerules; stamens 4–20 (rarely fewer), free, anthers extrorse, muticous; pollen grains 3-colporate, colpi operculate; ovary 2-locular, smooth; styles unlobed; fruit capsular, smooth or muricate, seeds carunculate; cotyledons much broader than radicle.

This subtribe includes three genera, one Eurasian and the other two South African.

KEY TO THE GENERA OF SUBTRIBE MERCURIALINAE

1a. Dioecious; stamens 8–20; pistillate flower with 2 subulate staminodia (or disk-segments); seeds carunculate ..... 160. *Mercurialis*
1b. Monoecious; stamens 2–7; pistillate staminodia absent or very small; seeds ecarunculate.
  2a. Capsule smooth; pistillate sepals 3; leaves entire or denticulate ..... 161. *Seidelia*
  2b. Capsule setose-muricate; pistillate sepals nearly obsolete; leaves crenulate ..... 162. *Leidesia*

160. Mercurialis L., Sp. Pl. 2: 1035. 1753; Gen. Pl. ed. 5, 437. 1754; Muell. Arg., DC. Prodr. 15(2): 794. 1866; Bentham, Gen. Pl. 3: 309. 1880; Pax & Hoffm., Pflanzenr. 147. VII (Heft 63): 271. 1914; Zimmermann et al., in Hegi, Ill. Fl. Mitteleur. 5(1): 126. 1925; Webster, J. Arnold Arbor. 48: 366. 1967; Tutin, Fl. Europaea 2: 212. 1968. TYPE: *Mercurialis perennis* L. [lectotype, designated by Small, in Britton & Brown, Ill. Fl. N. U.S. ed. 2, 2: 460. 1913].

A Eurasian genus of eight species, seven in Europe and Mediterranean Africa, and one in east temperate Asia.

161. Seidelia Baillon, Etude Gén. Euphorb. 465. 1858; Bentham, Gen. Pl. 3: 310. 1880; Prain, Ann. Bot. 27: 398. 1913; Pax & Hoffm., Pflanzenr. 147. VII (Heft 63): 282. 1914; Prain, Fl. Capensis 5(2): 464. 1920; Dyer, Gen. S. Afr. Fl. Pl., ed. 3, 316. 1975. TYPE: *Seidelia mercurialis* Baillon (nom. illeg.) [= *Seidelia triandra* (E. Mey.) Pax; lectotype, designated by Pfeiffer, Nomencl. Bot. 2: 1128. 1874].

A South African genus of two species.

162. Leidesia Muell. Arg., DC. Prodr. 15(2): 792. 1866; Bentham, Hook. Ic. Pl. 13: 66, t. 1284. 1879; Gen. Pl. 3: 310. 1880; Pax & Hoffm., Pflanzenr. 147. VII (Heft 63): 284. 1914; Prain, Ann. Bot. 27: 399. 1913; Fl. Capensis 5(2): 462. 1920; Dyer, Gen. S. Afr. Fl. Pl., ed. 3, 316. 1975. TYPE: *Leidesia obtusa* (Thunb.) Muell. Arg. [loc. cit. 793; lectotype, chosen here].

A South African genus of two or three species, very closely related to *Seidelia*; the two genera could certainly be combined without obscuring phylogeny. Although Pax & Hoffmann (1914) used the name *Leidesia procumbens* (L.) Prain for the two species of Mueller combined, this epithet belongs to the same taxon as *Leidesia capensis* Muell. Arg., which unfortunately is based on a confusion with *Urtica capensis* L. f. (a name referable to a species of *Acalypha*). It therefore seems better to choose Mueller's other species as lectotype.

Subtribe 30d. DYSOPSIDINAE Hurusawa, J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 6: 302. 1954. TYPE: *Dysopsis* Baillon.

Monoecious herbs; leaves alternate, simple, crenate, eglandular; stipules caducous; flowers axillary, mostly solitary; staminate calyx gamophyllous; stamens 3–6, interior connate; anthers apiculate, sacs adnate to connective; pollen grains globose, porate; pistillate sepals 3; ovary 3-locular, pubescent; styles unlobed, lacerate; fruit capsular; seeds with obsolete caruncle.

A monogeneric tribe of South America; closely related to the Mercurialinae, and further study may indicate that the two subtribes should be combined.

163. Dysopsis Baillon, Etude Gén. Euphorb. 435. 1858; Muell. Arg., DC. Prodr. 15(2): 949. 1866; Bentham, Gen. Pl. 3: 264. 1880; Grüning, Pflanzenr. 147. (Heft 58): 10. 1913; Pax & Hoffmann, Pflanzenr. 147. VII (Heft 63): 286. 1914. *Molina* Gay, Hist. Chile Bot. 5: 345. 1851 (non *Molina* Cav., 1790). TYPE: *Molina chilensis* Gay = *Dysopsis gayana* Baillon, nom. illeg. [= *Dysopsis glechomoides* (A. Rich.) Muell. Arg.].

A monotypic genus of the South American Andes (Ecuador to Chile), Juan Fernandez, and Costa Rica.

Subtribe 30e. CLEIDIINAE Webster, Taxon 24: 598. 1975. TYPE: *Cleidion* Blume.

Monoecious or dioecious trees or shrubs; indumentum simple; leaves alternate, simple, pinnately veined, with laminar glands, stipulate; inflorescences axillary, spicate or racemose; bracts eglandular; flowers apetalous, without disk; staminate sepals 3 or 4; stamens 25–80, free or basally connate; anthers muticous or apiculate; pollen grains 3-colporate, colpi not operculate; sexine rugulose-vermiculate, spinules vestigial; pistillode absent; pistillate sepals 3–6, imbricate; ovary (2-)3-locular; styles bifid, branches elongate; fruit capsular; seeds with dry or fleshy testa.

As here construed, subtribe Cleidiinae includes three genera, of which two are paleotropical and

the third pantropical. The characteristic globose pollen grains with vermiculate sexine ornamentation indicate an affinity between *Wetria* and *Cleidion* not clearly expressed in previous classifications. Pax & Hoffmann (1914) assigned *Wetria* to the series Trewiiformes adjacent to Alchorneae subtr. Conceveibinae; however, in those genera the indumentum is stellate and the pollen grains operculate.

KEY TO THE GENERA OF SUBTRIBE CLEIDIINAE

1a. Staminate flowers pedicellate, usually 2 or more per bract; stamens 25–80.
  2a. Anthers muticous, connective scarcely enlarged; stamens 25–30; pistillate pedicel less than 1 cm long ..... 164. *Wetria*
  2b. Anthers apiculate, connective enlarged; stamens mostly 30–80 or more; pistillate pedicel over 1 cm long ..... 165. *Cleidion*
1b. Staminate flowers sessile, 1 per bract; stamens 15–25, anthers apiculate, connective not enlarged ..... 166. *Sampantaea*

164. Wetria Baillon, Etude Gén. Euphorb. 409. 1858; J. J. Smith, Med. Dept. Landb. 10: 470. 1910; Pax & Hoffm., Pflanzenr. VII (Heft 63): 219. 1914; Backer & Bakhuizen, Fl. Java 1: 485. 1963; Airy Shaw, Kew Bull. 26: 350. 1972; Whitmore, Tree Fl. Malaya 2: 136. 1973; Airy Shaw, Kew Bull. 36: 358. 1981. TYPE: *Wetria trewioides* Baillon, nom. illeg. [= *Wetria insignis* (Steud.) Airy Shaw].

A monotypic genus, the single species occurring from Burma to Indonesia and New Guinea. Airy Shaw has suggested that the genus is closely related to *Alchornea*, but it differs in its simple indumentum, bifid styles, and larger stamen number.

165. Cleidion Blume, Bijdr. Fl. Ned. Ind. 612. 1826; Muell. Arg., DC. Prodr. 15(2): 983. 1866; Bentham, Gen. Pl. 3: 320. 1880; Pax & Hoffm., Pflanzenr. 147. VII (Heft 63): 288. 1914; Croizat, J. Arnold Arbor. 24: 166. 1943; Léonard, Bull. Jard. Bot. Nat. Belge 42: 297. 1972; Leandri, Adansonia II. 12: 193. 1972; A. C. Smith, Fl. Vitiensis Nova 2: 514. 1981; McPherson & Tirel, Fl. Nouv.-Caléd. 14: 143. 1987; Huft, Ann. Missouri Bot. Gard. 75: 1103. 1989. TYPE: *Cleidion javanicum* Blume.

Redia Casaretto, Nov. Stirp. Bras. 51. 1843. TYPE: *Redia tricocca* Casar. [= *Cleidion tricoccum* (Casar.) Baillon].

Psilostachys Turcz., Bull. Soc. Imp. Naturalistes Moscou 16: 58. 1843. TYPE: *Psilostachys axillaris* Turcz. [= *Cleidion tricoccum* (Casar.) Baillon].

Lasiostyles Presl, Abh. Königl. Böhm. Ges. Wiss. V. 3: 579. 1845. TYPE: *Lasiostyles salicifolia* Presl [= *Cleidion javanicum* Blume].

Tetraglossa Beddome, Madras J. Lit. Sci. II. 22: 70. 1861. TYPE: *Tetraglossa indica* Beddome [= *Cleidion javanicum* Blume].

A well-marked genus of ca. 25 species, of which 5 are neotropical, 1 west African, 12 New Caledonian, and the remainder tropical Asian.

166. Sampantaea Airy Shaw, Kew Bull. 26: 328. 1972; Hook. Ic. Pl. 38: t. 3717. 1974. TYPE: *Sampantaea amentiflora* (Airy Shaw) Airy Shaw.

A monotypic genus restricted to Thailand and Cambodia. It appears closely related to *Wetria* and may prove congeneric.

Subtribe 30f. MACARANGINAE (Hutchinson) Webster, Taxon 24: 598. 1975. Tribe Macarangeae Hutchinson, Amer. J. Bot. 56: 755. 1969. TYPE: *Macaranga* Du Petit Thouars.

Dioecious trees or shrubs; indumentum simple; leaves alternate, unlobed or palmately lobed, pinnately to palmately veined, glandular or eglandular; stipules minute to enlarged; inflorescences axillary, racemose or paniculate; bracts ± glandular; flowers apetalous and lacking disk; staminate calyx of 2–5 segments; stamens (1)2–50, free; anthers muticous, 2–4-valved; pollen grains 3- or 4-colporate, sexine finely to coarsely rugulose-spinulose; pistillate sepals 3–5, free or connate; ovary (1-)2- or 3-(–6)locular; styles unlobed; fruit capsular; seeds ecarunculate, testa fleshy.

As defined by Webster (1975) and here, subtribe Macaranginae is much more narrowly defined than Hutchinson's tribe Macarangeae, which included seven other genera from various tribes of subfamilies Acalyphoideae and Crotonoideae; only the genus *Macaranga* is included here.

167. Macaranga Du Petit Thouars, Gen. Nova Madag. 26. 1806; Muell. Arg., DC. Prodr. 15(2): 987. 1866; Bentham, Gen. Pl. 3: 320. 1880; Hook. f., Fl. Brit. Ind. 5: 445. 1887; Pax & Hoffm., Pflanzenr. 147. VII (Heft 63): 298. 1914; Gagnepain, Fl. Indochine 5: 434. 1926; Perry, J. Arnold Arbor. 34: 191. 1953; Whitmore, Tree Fl. Malaya 2: 105. 1973; Kew Bull. Add. Ser. 4: 140. 1975; Kew Bull. Add. Ser. 8: 123. 1980; A. C. Smith, Fl. Vitiensis Nova 2: 500. 1981; Coode, Taxon

25: 184. 1976; McPherson & Tirel, Fl. Nouv.-Caléd. 14: 172. 1987; Radcliffe-Smith, Fl. E. Trop. Afr. Euphorb. 1: 239. 1987. TYPE: *Macaranga mauritiana* Bojer ex Muell. Arg. [lectotype, selected by Coode, 1976, who rejected the proposed selection of *M. roxburgii* Wight by Wheeler, 1975].

Mappa A. Jussieu, Euphorb. Tent. 44. 1824. TYPE: *Mappa glabra* A. Juss. [= *Macaranga glabra* (A. Juss.) Pax & Hoffm.].

Pachystemon Blume, Bijdr. Fl. Ned. Ind. 626. 1826. TYPE: *Pachystemon trilobum* (Reinw. ex Bl.) Bl. [= *Macaranga triloba* (Reinw. ex Bl.) Muell. Arg.].

Mecostylis Kurz ex Teysmann & Binnendijk, Natuurk. Tijdschr. Ned.-Indië 27: 44. 1864. TYPE: *Mecostylis acalyphoides* Kurz ex Teysm. & Binn. [= *Macaranga involucrata* (Roxb.) Baillon].

Phocea Seemann, J. Bot. 8: 69. 1870. TYPE: *Phocea andersonii* Seem. [= *Macaranga* sp.; not identified by Pax & Hoffm., 1931, or McPherson & Tirel, 1987].

A very large and diverse paleotropical genus of ca. 300 species; there are about 50 species in Africa/Madagascar, over 200 in tropical Asia from India to New Guinea, and a few in Fiji and other Pacific islands. The genus has acquired several generic synonyms, but no plausible system of segregate genera has ever been proposed.

Subtribe 30g. CLAOXYLINAE Hurusawa, J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 6: 301. 1954. Tribe Acalypheae subtribe Mercurialinae series Claoxyliformes Pax & Hoffm., Pflanzenr. 147. VII (Heft 63): 75. 1914. Tribe Claoxyleae Hutchinson, Amer. J. Bot. 56: 752. 1969. TYPE: *Claoxylon* A. Juss.

Tribe Mareyeae Hutchinson, Amer. J. Bot. 56: 751. 1969. TYPE: *Mareya* Baillon.

Monoecious or dioecious trees, shrubs, or herbs; indumentum simple; leaves alternate, unlobed, mostly dentate, pinnately veined, without laminar glands; stipules small, persistent or deciduous; inflorescences axillary, racemose or paniculate; bracts eglandular; flowers apetalous; staminate sepals 2–5; disk mostly of interstaminal processes or annular (rarely absent); stamens 5–40(–200), free; anther sacs separated to the connective, ± erect; pollen grains rugulose-spinulose; pistillate sepals 2–4, open or imbricate; disk annular or dissected; ovary mostly 2- or 3-locular; styles ± elongated, unlobed but lacerate; fruit capsular; seeds ecarunculate, testa usually fleshy.

A paleotropical subtribe of nine genera, some hardly distinct, and others not certainly belonging here.

KEY TO THE GENERA OF SUBTRIBE CLAOXYLINAE

1a. Styles undivided; pistillate disk unlobed to 5-lobed.
  2a. Buds perulate; stipules mostly persistent ..... 168. *Erythrococca*
  2b. Buds not perulate; stipules mostly deciduous.
    3a. Racemes uniformly floriferous; capsules coriaceous; leaves not stipellate.
      4a. Staminate disk of interstaminal segments.
        5a. Anther sacs erect; mostly dioecious.
          6a. Stamens mostly 20 or more; styles recurved, papillose but hardly lacerate ..... 169. *Claoxylon*
          6b. Stamens up to 15; styles erect, lacerate ..... 170. *Claoxylopsis*
        5b. Anther sacs pendent; styles lacerate; stamens 10–40; monoecious ..... 171. *Mareya*
      4b. Staminate disk urceolate; stamens 6–12; styles recurved, lacerate ..... 172. *Discoclaoxylon*
    3b. Racemes interrupted; capsules crustaceous; leaves stipellate ..... 173. *Micrococca*
1b. Styles bifid; pistillate disk 8–10-lobed; staminate disk of interstaminal segments; stamens up to 25; seed-coat not fleshy ..... 174. *Amyrea*

168. Erythrococca Bentham, Niger Fl. 506. 1849; Muell. Arg., DC. Prodr. 15(2): 790. 1866; Bentham, Gen. Pl. 3: 308. 1880; Prain, Ann. Bot. 25: 606. 1911; Fl. Trop. Afr. 6(1): 847. 1912; Pax & Hoffm., Pflanzenr. 147. VII (Heft 63): 86. 1914; Keay, Fl. W. Trop. Afr. ed. 2, 1: 400. 1954; Radcliffe-Smith, Fl. E. Trop. Afr. Euphorb. 1: 265. 1987. TYPE: *Erythrococca aculeata* Benth., nom. illeg. [= *Erythrococca anomala* (Juss. ex Poir.) Prain].

Poggeophyton Pax, Bot. Jahrb. 19: 88. 1894. TYPE: *Poggeophyton aculeatum* Pax [= *Erythrococca poggeophyton* Prain].

Chloropatane Engler, Bot. Jahrb. 26: 383. 1899. TYPE: *Chloropatane africana* (Baillon) Engler [= *Erythrococca africana* (Baillon) Prain].

Athroandra (Hook. f.) Pax & Hoffm., Pflanzenr. 147. VII (Heft 63): 76. 1914. TYPE: *Claoxylon mannii* Hook. f. [= *Erythrococca mannii* (Hook. f.) Prain].

A diverse African genus of ca. 50 species, whose delimitation apparently requires further analysis. Although Prain, Keay, and Radcliffe-Smith treat *Athroandra* as part of *Erythrococca*, Airy Shaw

(1966) suggested that *Erythrococca* is close to *Claoxylon*.

169. Claoxylon A. Jussieu, Euphorb. Tent. 43. 1824; Muell. Arg., DC. Prodr. 15(2): 775. 1866; Bentham, Gen. Pl. 3: 309. 1880; Pax & Hoffm., Pflanzenr. 147. VII (Heft 63): 100. 1914; Merrill, Enum. Phil. Pl. 2: 429. 1923; Whitmore, Tree Fl. Malaya 2: 78. 1973; A. C. Smith, Fl. Vit. Nova 2: 516. 1981. TYPE: *Claoxylon parviflorum* A. Juss.

Erytrochilus Reinw. ex Blume, Bijdr. Fl. Ned.-Ind. 614. 1826. TYPE: *Erytrochilus indicus* Reinw. ex Bl. [= *Claoxylon indicum* (Reinw. ex Bl.) Hassk.; designated by Wheeler, 1975].

Quadrasia Elmer, Leafl. Phil. Bot. 7: 2656. 1915. TYPE: *Quadrasia euphorbioides* Elmer [= *Claoxylon euphorbioides* (Elmer) Merr.].

A paleotropical genus of ca. 75 species, absent from Africa but extending from Madagascar to Melanesia and Hawaii.

170. Claoxylopsis Leandri, Bull. Soc. Bot. France 85: 526. 1938; Radcliffe-Smith, Kew Bull. 43: 642. 1988. TYPE: *Claoxylopsis perrieri* Leandri.

A genus of three species endemic to Madagascar. Although apparently very close to *Claoxylon*, it is still poorly known and its position and status must be regarded as tentative.

171. Mareya Baillon, Adansonia I. 1: 73. 1860; Muell. Arg., DC. Prodr. 15(2): 792. 1866; Bentham, Hook. Ic. Pl. 13: 63, t. 128. 1879; Gen. Pl. 3: 312. 1880; Prain, Fl. Trop. Afr. 6(1): 910. 1912; Pax & Hoffm., Pflanzenr. 147. XIV (Heft 68): 11. 1919; Léonard, Bull. Jard. Bot. Brux. 25: 291. 1945; Radcliffe-Smith, Fl. E. Trop. Afr. Euphorb. 1: 216. 1987. TYPE: *Mareya spicata* Baillon.

Mareyopsis Pax & Hoffm., Pflanzenr. 147. XIV (Heft 68): 13. 1919. TYPE: *Mareyopsis longifolia* (Pax) Pax & Hoffm. [= *Mareya longifolia* Pax].

An African genus of three species.

172. Discoclaoxylon (Muell. Arg.) Pax & Hoffmann, Wiss. Ergebn. Deutsche Zentral-Afr. Exped. 2: 452. 1912; Pflanzenr. 147. VII (Heft 63): 137. 1914; Radcliffe-Smith, Fl. E. Trop. Afr. Euphorb. 1: 279. 1987. *Claoxylon* sect. *Discoclaoxylon* Muell. Arg., Flora 47: 137. 1864. TYPE: *Discoclaoxylon hexandrum* (Muell. Arg.) Pax & Hoffm. [lectotype, chosen here; the larger staminate disk in the lectotype species appropriately reflects the taxon name].

A mainly west African genus of three species, extending from Sierra Leone and Fernando Póo to Uganda.

173. Micrococca Bentham, Niger Fl. 503. 1849; Gen. Pl. 3: 309. 1880; Prain, Ann. Bot. 25: 628. 1911; Fl. Trop. Afr. 6(1): 876. 1912; Airy Shaw, Kew Bull. 25: 524. 1971; Dyer, Gen. S. Afr. Fl. Pl., ed. 3, 1: 315. 1975; Radcliffe-Smith, Fl. E. Trop. Afr. Euphorb. 1: 260. 1987. TYPE: *Micrococca mercurialis* (L.) Benth.

A paleotropical genus of 12 species, reported from tropical Africa and Madagascar to Malaya.

174. Amyrea Leandri, Notul. Syst. (Paris) 9: 168. 1940. TYPE: *Amyrea sambiranensis* Leandri [lectotype, selected here].

A genus of two species endemic to Madagascar. *Amyrea* diverges from all of the other genera of subtribe Claoxylinae in its bifid styles, and its position requires evaluation.

Subtribe 30h. LOBANILIINAE Radcliffe-Smith, Kew Bull. 44: 339. 1989. TYPE: *Lobanilia* Radcl.-Sm.

Dioecious trees or shrubs; indumentum stellate (sometimes simple as well); leaves alternate, unlobed, mostly pinnately veined, without embedded or granular laminar glands; stipules minute and deciduous; inflorescences axillary, racemose; flowers apetalous; staminate sepals 3: disk of interstaminal segments; stamens 17–30, free; anther-sacs free to base; pistillate sepals 3; disk annular or ± dissected; ovary 3–4-locular; styles unlobed, papillose or plumose; fruit capsular; seeds ecarunculate.

This monotypic subtribe, recently proposed by Radcliffe-Smith, appears very similar to subtribe Claoxylinae except for the stellate indumentum. It is provisionally recognized here until detailed comparisons with taxa of Claoxylinae can be made to determine whether *Lobanilia* should be kept in a separate subtribe.

175. Lobanilia Radcliffe-Smith, Kew Bull. 44: 334. 1989. TYPE: *Lobanilia luteobrunnea* (Baker) Radcl.-Sm.

A genus of seven species confined to Madagascar. Originally these were treated as a section of

Claoxylon, but Radcliffe-Smith presented persuasive arguments for recognition of a separate genus.

Subtribe 30i. ROTTLERINAE Meisner, Pl. Vasc. Gen. 1: 339. 1841; Webster, Taxon 24: 598. 1975. TYPE: *Rottlera* Roxb. [= *Mallotus* L.].

Family Trewiaceae Lindley, Intr. Nat. Syst. ed. 2, 174. 1835. Acalypheae subtribe Mercurialinae series Trewiiformes Pax & Hoffm., Pflanzenr. 147. VII (Heft 63): 139. 1914. TYPE: *Trewia* L.

Tribe Acalypheae subtribe Coelodisceae Muell. Arg., Linnaea 34: 143. 1865. TYPE: *Coelodiscus* Baillon [= *Mallotus* Lour.].

Tribe Malloteae Hutchinson, Amer. J. Bot. 56: 752. 1969. TYPE: *Mallotus* Lour.

Dioecious (rarely monoecious) trees or shrubs; indumentum stellate (rarely simple); leaves alternate or opposite, unlobed or lobed, pinnately or palmately veined, sometimes with embedded laminar glands; stipules present or obsolete; inflorescences terminal or axillary, racemose or paniculate; flowers apetalous; staminate sepals 3–5; disk intrastaminal, of interstaminal segments, or absent; stamens 15–300, free; anthers muticous, anther-sacs not pendulous; pollen grains 3(–4) colporate, finely to coarsely tectate-perforate and spinulose; pistillate sepals 3–6(–10), free or connate; disk absent; ovary 2–4(–8)-locular, sometimes echinate; styles unlobed, ± plumose or laciniate; fruit capsular or baccate; seeds ecarunculate (rarely carunculate), testa often fleshy.

This Old World subtribe of eight closely related genera is most strongly represented in tropical Asia.

KEY TO THE GENERA OF SUBTRIBE ROTTLERINAE

1a. Carpels 2–4 (rarely 5); fruit capsular or drupaceous.
  2a. Styles unlobed; leaves usually glandular.
    3a. Fruit capsular, dehiscent; pistillate sepals free or connate.
      4a. Ovary smooth to echinate, not winged; inflorescences terminal or opposite leaves (sometimes axillary as well); bracts small; stamens 20–200; pollen sexine tectate-perforate to rugulose.
        5a. Styles elongate; leaves usually granulose-glandular ..... 176. *Mallotus*
        5b. Styles contracted; leaves eglandular ..... 177. *Deuteromallotus*
      4b. Ovary ± winged; inflorescences axillary.
        6a. Stamens many (over 200); seeds ecarunculate ..... 178. *Cordemoya*
        6b. Stamens 15–20; seeds carunculate ..... 179. *Coccoceras*
    3b. Fruit indehiscent; pistillate calyx gamophyllous.
      7a. Staminate disk absent; ovary 2–4-locular ..... 180. *Trewia*
      7b. Staminate disk present; ovary 1(2)-locular ..... 181. *Neotrewia*
  2b. Styles bifid; leaves eglandular ..... 182. *Rockinghamia*
1b. Ovary 8-locular; fruit baccate; leaves alternate, glandular; stamens 15–20 ..... 183. *Octospermum*

176. Mallotus Loureiro, Fl. Cochinch. 635. 1790; Muell. Arg., DC. Prodr. 15(2): 956. 1866; Bentham, Fl. Austral. 6: 138. 1873; Gen. Pl. 3: 319. 1880; Forbes & Hemsley, J. Linn. Soc. Bot. 26: 439. 1894; Schum. & Lauterb., Fl. Deutsche Schutzgeb. 394. 1901; J. J. Smith, Meded. Dept. Landb. 10: 394. 1910; Prain, Fl. Trop. Afr. 6(1): 927. 1912; Pax & Hoffm., Pflanzenr. 147. VII (Heft 63): 145. 1914; Natürl. Pflanzenfam. ed. 2, 19c: 113. 1931; Merrill & van Steenis, Webbia 8: 405. 1951; Hurusawa, J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 6: 304. 1954; Airy Shaw, Kew Bull. 20: 41. 1866; 21: 379. 1968; 25: 526. 1971; Whitmore, Tree Fl. Malaya 2: 113. 1973; Airy Shaw, Kew Bull. Add. Ser. 4: 160. 1975; 8: 162. 1980; Radcliffe-Smith, Fl. E. Trop. Afr. Euphorb. 1: 235. 1987. TYPE: *Mallotus cochinchensis* Lour.

Echinus Loureiro, Fl. Cochinch. 633. 1790. TYPE: *Echinus trisulcus* Lour. [= *Mallotus cochinchensis* Lour.].

Rottlera Roxburgh, Pl. Coromandel 2: 36. 1798 (non Willd., 1797). TYPE: *Rottlera tinctoria* Roxb. [= *Mallotus philippensis* (Lam.) Muell. Arg.].

Adisca Blume, Bijdr. Fl. Ned. Ind. 609. 1826. TYPE: *Adisca floribunda* Bl. [= *Mallotus floribundus* (Bl.) Muell. Arg.; lectotype, chosen here].

Plagianthera Reichb. f. & Zollinger, Verh. Natuurk. Ver. Ned. Ind. 1(4): 19. 1856. TYPE: *Plagianthera oppositifolia* (Bl.) Reichb. f. & Zoll. [= *Mallotus blumeanus* Muell. Arg.].

Hancea Seemann, Bot. Voy. Herald 409. 1857. TYPE: *Hancea hookeriana* Seem. [= *Mallotus hookerianus* (Seem.) Muell. Arg.].

Axenfeldia Baillon, Etude Gén. Euphorb. 419. 1858. TYPE: *Axenfeldia intermedia* Baillon [= *Mallotus muricatus* (Wight) Muell. Arg.].

Coelodiscus Baillon, Etude Gén. Euphorb. 293. 1858. TYPE: *Ricinus dioicus* Wall. ex Baill. [= *Mallotus eriocarpus* (Thw.) Muell. Arg.].

Aconceveibum Miquel, Fl. Ind. Bat. 1(2): 389. 1859. TYPE: *Aconceveibum trinerve* Miq. [= *Mallotus philippensis* (Lam.) Muell. Arg.].

Echinocroton F. Mueller, Fragm. Phytogeogr. Austral.

1: 31. 1859. TYPE: *Echinocroton claoxyloides* F. Muell. [= *Mallotus claoxyloides* (F. Muell.) Muell. Arg.].

Diplochlamys Muell. Arg., Flora 47: 539. 1864. TYPE: *Diplochlamys griffithianus* Muell. Arg. [= *Mallotus griffithianus* (Muell. Arg.) Hook. f.].

This large and complex paleotropical genus includes ca. 150 species, of which there are only two in Africa and Madagascar, the rest in Asia and Australasia (to Fiji).

177. Deuteromallotus Pax & Hoffmann, Pflanzenr. 147. VII (Heft 63): 212. 1914; Leandri, Bull. Soc. Bot. France 103: 605. 1956. TYPE: *Deuteromallotus acuminatus* (Baillon) Pax & Hoffm.

A genus of two species endemic to Madagascar.

178. Cordemoya Baillon, Adansonia I. 1: 255. 1861; Pax & Hoffm., Pflanzenr. 147. VII (Heft 63): 208. 1914. TYPE: *Cordemoya integrifolia* Willd. ex Baill. [lectotype].

A monotypic genus endemic to Malagasia.

179. Coccoceras Miquel, Fl. Ind. Batav. Suppl. 455. 1860; Muell. Arg., DC. Prodr. 15(2): 949. 1866; Bentham, Gen. Pl. 3: 308. 1880; Pax & Hoffm., Pflanzenr. 147. VII (Heft 63): 209. 1914; Airy Shaw, Kew Bull. 16: 349. 1963. TYPE: *Coccoceras sumatranus* Miq.

A tropical Asian genus of three or four species, distributed from Burma to Borneo. Airy Shaw (1963) reduced *Coccoceras* to a section of *Mallotus*, perhaps correctly so.

180. Trewia L., Sp. Pl. 1193. 1753; Klotzsch, Arch. Naturgesch. 7: 255. 1841; Muell. Arg., DC. Prodr. 15(2): 953. 1866; Bentham, Gen. Pl. 3: 318. 1880; J. J. Smith, Meded. Dept. Landb. 10: 389. 1910; Pax & Hoffm., Pflanzenr. 147. VII (Heft 63): 140. 1914; Airy Shaw, Kew Bull. 20: 406. 1966; Kew Bull. Add. Ser. 4: 200. 1975. TYPE: *Trewia nudiflora* L.

A monotypic genus, the single species widely distributed from India to southern China and Indonesia.

181. Neotrewia Pax & Hoffmann, Pflanzenr. 147. VII (Heft 63): 211. 1914; Merrill, Enum. Phil. Pl. 2: 437. 1923. TYPE: *Neotrewia cumingii* (Muell. Arg.) Pax & Hoffm.

A monotypic genus of the Philippines and Celebes, dubiously separable from *Trewia*.

182. Rockinghamia Airy Shaw, Kew Bull. 20: 29. 1966; 35: 667. 1980. TYPE: *Rockinghamia angustifolia* (Benth.) Airy Shaw.

A genus of two species endemic to tropical Australia (Queensland).

183. Octospermum Airy Shaw, Kew Bull. 19: 311. 1965; Hook. Ic. Pl. 38: t. 3716. 1974; Kew Bull. Add. Ser. 8: 176. 1980. TYPE: *Octospermum pleiogynum* (Pax & Hoffm.) Airy Shaw.

A single species of New Guinea.

Subtribe 30j. ACALYPHINAE Grisebach, Fl. Br. W. Ind. 45. 1859; Pax & Hoffm., Pflanzenr. 147. XVI (Heft 85): 1. 1924. TYPE: *Acalypha* L.

Monoecious or dioecious trees, shrubs, or herbs; indumentum simple or stellate, often glandular; leaves alternate, unlobed, pinnately or palmately veined, stipulate; inflorescences spicate or the pistillate (in a few species) paniculate, terminal or axillary, unisexual or bisexual; pistillate bracts usually enlarged in fruit; staminate sepals 4; disk absent; stamens usually 8, filaments free, anther sacs pendulous and vermiform; pollen grains porate, rugulose; pistillate sepals 3–5, imbricate; disk absent; ovary (2-)3-locular; styles mostly free, laciniate (rarely entire); fruit capsular; seeds with caruncle minute or absent.

As here defined, subtribe Acalyphinae includes only the genus *Acalypha*; it appears closely related to subtribe Claoxylinae, but differs in its unique anthers, enlarged pistillate bracts, distinctive porate pollen, and dissected styles.

184. Acalypha L., Sp. Pl. 1003. 1753; Gen. Pl. ed. 5, 436. 1754; Muell. Arg., DC. Prodr. 15(2): 799. 1866; Bentham, Gen. Pl. 3: 311. 1880; Hutchinson, Fl. Trop. Afr. 6(1): 880. 1912; Pax & Hoffm., Pflanzenr. 147. XVI (Heft 85): 12. 1924; Natürl. Pflanzenfam. ed. 2, 19c: 134. 1931; Hurusawa, J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 6: 295. 1954; Webster, J. Arnold Arbor. 48: 370. 1967; A. C. Smith, Fl. Vit. Nova 2: 522. 1981; Seberg, Nordic J. Bot. 4: 159. 1984; Radcliffe-Smith, Fl. E. Trop. Afr. Euphorb. 1: 185. 1987. TYPE: *Acalypha virginica* L. [lectotype, designated by Small, in Britton & Brown, Ill. Fl. N. U.S. ed. 2, 2: 457. 1913].

Caturus L., Syst. Nat. ed. 12, 2: 650. 1767; Mant. Pl. 19, 127. 1767. TYPE: *Caturus spiciflora* L. [= *Acalypha hispida* Burm. f.].

Linostachys Klotzsch ex Schlect., Linnaea 19: 235. 1846. TYPE: *Linostachys padifolia* Schlecht. [= *Acalypha schlechtendaliana* Muell. Arg.].

Odonteilema Turczaninov, Bull. Soc. Imp. Natur. Moscou 21: 587. 1848. TYPE: *Odonteilema claussenii* Turcz. [= *Acalypha claussenii* (Turcz.) Muell. Arg.].

Gymnalypha Grisebach, Bonplandia 6: 2. 1858. TYPE: *Gymnalypha jacquinii* Griseb., nom. illeg. [= *Acalypha villosa* Jacq.].

Corythea S. Watson, Proc. Amer. Acad. Sci. 22: 451. 1887. TYPE: *Corythea filipes* S. Wats. [= *Acalypha filipes* (S. Watson) McVaugh].

Acalyphopsis Pax & Hoffm., Pflanzenr. 147. XVI (Heft 85): 178. 1924. TYPE: *Acalyphopsis celebica* Pax & Hoffm. [= *Acalypha hoffmanniana* Hurus.].

With ca. 450 species, *Acalypha* is the fourth largest genus of Euphorbiaceae; in addition to the small number of temperate species, species are widespread throughout the tropics except in Hawaii and a few Pacific archipelagos.

Subtribe 30k. LASIOCOCCINAE Webster, Taxon 24: 597. 1975. TYPE: *Lasiococca* Hook. f.

Monoecious or dioecious trees or shrubs; indumentum simple or lepidote; leaves alternate, unlobed, pinnately veined; eglandular, stipulate; inflorescences axillary, unisexual, racemose or the pistillate flowers solitary, bracts eglandular; staminate sepals usually 3; disk absent; stamens many, filaments connate, anthers on filaments of branching fascicles; pollen grains 3-colporate; not operculate; pistillate sepals 5–8, imbricate; disk absent; ovary 3-locular; styles unlobed, smooth to papillose or plumose; fruit capsular; seeds ecarunculate, testa usually fleshy.

This subtribe includes three genera that were treated by Pax & Hoffmann (1919) as part of subtribe Ricininae, doubtlessly because of the androecium of many stamens with anthers borne on branches of a dendritic column. However, this character almost surely represents a convergence, since the Lasiococcinae diverge from *Ricinus* in many important characters, including ecarunculate seeds, pinnately veined unlobed leaves, and axillary inflorescences. Airy Shaw (1974) has suggested a close relationship of subtribe Lasiococcinae to *Mallotus*.

KEY TO THE GENERA OF SUBTRIBE LASIOCOCCINAE

1a. Monoecious; pistillate sepals persistent; indumentum simple; ovary muricate ___ 185. *Lasiococca*

1b. Dioecious; pistillate sepals deciduous; indumentum simple or lepidote.

2a. Lepidote scales absent; ovary tuberculate; pollen sexine not striate ___ 186. *Spathiostemon*

2b. Lepidote scales present; ovary smooth; pollen sexine striate ___ 187. *Homonoia*

185. Lasiococca Hooker f., Hook. Ic. Pl. 16: t. 1587. 1887; Fl. Brit. Ind. 5: 456. 1887; Haines, Kew Bull. Misc. Inf. 1920; 70. 1920; Airy Shaw, Kew Bull. 16: 358. 1963; 21: 406. 1968; Whitmore, Tree Fl. Malaya 2: 104. 1973; Thin, J. Biol. Sinh Hoc 8(3): 36. 1986. TYPE: *Lasiococca symphyllifolia* (Kurz) Hook. f.

A tropical Asian genus of three species, with a disjunct distribution in India, Malaya and Indochina, and Hainan.

186. Spathiostemon Blume, Bijdr. Fl. Ned. Ind. 621. 1826; Airy Shaw, Kew Bull. 16: 357. 1963; 20: 408. 1966; 26: 341. 1972; Hook. Ic. Pl. 38: t. 3720. 1974; Kew Bull. Add. Ser. 4: 196. 1975; 8: 202. 1980. TYPE: *Spathiostemon javense* Bl.

Polydragma Hook. f., Hook. Ic. Pl. 18: t. 1701. 1887; Fl. Brit. Ind. 5: 456. 1887. TYPE: *Polydragma mallotiforme* Hook. f. [= *Spathiostemon javense* Bl.].

Clonostylis Sp. Moore, J. Bot. 63 (suppl.): 101. 1925. TYPE: *Clonostylis forbesii* Sp. Moore [= *Spathiostemon forbesii* (Sp. Moore) Airy Shaw].

A genus of two species distributed from Thailand to the Philippines and New Guinea. Although united with *Homonoia* by Mueller (1866), Bentham (1880), and Pax & Hoffmann (1919), it may be distinct, as indicated by Airy Shaw.

187. Homonoia Loureiro, Fl. Cochinch. 636. 1790; Muell. Arg., DC. Prodr. 15(2): 1022. 1866; Bentham, Gen. Pl. 3: 322. 1880; J. J. Smith, Med. Dept. Landb. 10: 542. 1910; Pax & Hoffm., Pflanzenr. 147. XI (Heft 68): 114. 1919; Gagnepain, Fl. Indochine 5: 330. 1925; Airy Shaw, Kew Bull. Add. Ser. 4: 136. 1975; Kew Bull. 36: 310. 1981. TYPE: *Homonoia riparia* Lour.

Lumanaja Blanco, Fl. Filip. 821. 1837. TYPE: *Lumanaja fluviatilis* Blanco [= *Homonoia riparia* Lour.].

A genus of two Asian species (India to Taiwan, the Philippines, and New Guinea).

Tribe 31. PLUKENETIEAE (Bentham) Hutchinson, Amer. J. Bot. 56: 753. 1969. Crotoneae subtribe Plukenetieae Bentham, Gen. Pl. 3: 252. 1880. TYPE: *Plukenetia* L.

Monoecious (rarely dioecious) trees, shrubs, or herbs, sometimes climbing or twining; indumentum simple, often glandular, sometimes urticant; leaves alternate, unlobed to palmately parted, pinnately to palmately veined, sometimes glandular or sti-

pellate at base; stipules present. Inflorescences terminal or axillary, usually bisexual, mostly racemose or spicate; bracts eglandular; flowers apetalous. Staminate calyx splitting into 3–5 valvate segments; disk interstaminal, extrastaminal, or absent; stamens (2)3–100, usually free; anthers introrse or extrorse, muticous or apiculate; pollen grains 3-colporate, porate, or inaperturate, sexine varying from tectate to intectate; pistillode absent. Pistillate sepals 3–6, imbricate; disk absent; ovary 3- or 4-locular; styles unlobed, slender or dilated, sometimes papillose or lacerate, usually connate into a distinct column. Fruit capsular; columella persistent; seeds ecarunculate, testa usually dry; endosperm copious; cotyledons much longer and broader than radicle.

This distinctive tribe includes 16 genera with more than 250 species in the tropics of both the Old World and New World; the majority are neotropical.

KEY TO THE SUBTRIBES OF TRIBE PLUKENETIEAE

1a. Flowers in racemes or spikes, not bibracteate pseudanthia; pollen grains subglobose.
  2a. Stinging hairs absent; fruit winged, crested, carinate, or indehiscent; pollen grains 3-colpate ..... 31a. Plukenetiinae
  2b. Stinging hairs present; fruit usually unappendaged; pollen grains 3-colpate, 3-porate, or inaperturate, rugulose ..... 31b. Tragiinae
1b. Flowers in bibracteate pseudanthia; pollen grains prolate, coarsely reticulate; stinging hairs present ..... 31c. Dalechampiinae

Subtribe 31a. PLUKENETIINAE Bentham, Gen. Pl. 3: 253. 1880; Pax, Natürl. Pflanzenfam. ed. 1, 3(5): 62. 1890; Pax & Hoffm., Pflanzenr. 147. IX (Heft 68): 1. 1919; Natürl. Pflanzenfam. ed. 2, 19c: 141. 1931; Webster, Taxon 24: 598. 1975. TYPE: *Plukenetia* L.

Trees, shrubs, lianas, or twining vines; indumentum entirely of simple hairs; leaf blades simple and unlobed, entire or dentate, often with embedded laminar glands, sometimes stipellate; inflorescence axillary or terminal and appearing leaf-opposed; stamens 4–50, filaments free or anthers subsessile; pollen grains suboblate to subglobose, tricolpate, tectate-perforate to semitectate-reticulate; ovary 3- or 4-locular, often winged; styles massive, partly to entirely connate; fruit capsular or rarely indehiscent.

As delimited by Webster (1975), subtribe Plukenetiinae is here treated in a narrower sense than the concepts of Bentham (1880) or Pax & Hoffmann (1919, 1931). In contrast to subtribe Tragiinae, the distribution of the Plukenetieae is almost entirely neotropical (a few species of *Plukenetia* occur in Africa).

KEY TO THE GENERA OF SUBTRIBE PLUKENETIINAE

1a. Ovary 3-locular; pistillate sepals 5 or 6; trees, shrubs or vines.
  2a. Stamens 4; staminate disk segments 4 (or if absent replaced by 4-lobed pseudodisk); leaves pinnately veined; trees or shrubs.
    3a. Disk absent; base of stamens dilated, forming an intrastaminal pseudodisk; style urceolate ..... 188. *Haematostemon*
    3b. Disk extrastaminal; style ovoid ..... 189. *Astrococcus*
  2b. Stamens 10 or more; staminate disk segments absent or minute, numerous.
    4a. Stamens ca. 20; style urceolate; flowers fasciculate in leaf axils; leaves pinnately veined; tree or shrub ..... 190. *Angostyles*
    4b. Stamens 10; style cylindrical, clavate, apically 3-lobed; flowers in axillary racemes; leaves palmately veined; twining vine ..... 191. *Romanoa*
1b. Ovary 4-locular; pistillate sepals 4; twining vines or lianas.
  5a. Styles mostly free, connate for less than one-half their length, tips bifid; stamens 40 50 ..... 192. *Eleutherostigma*
  5b. Styles entirely connate into a massive column; stamens 8–30(–40).
    6a. Fruit dehiscent (rarely indehiscent, but then staminate receptacle not globose) ..... 193. *Plukenetia*
    6b. Fruit indehiscent; staminate receptacle globose ..... 194. *Vigia*

188. Haematostemon (Muell. Arg.) Pax & Hoffmann, Pflanzenr. 147. IX (Heft 68): 31. 1919; Sandwith, Kew Bull. 1950: 133. 1951; Jablonski, Mem. New York Bot. Gard. 17: 143. 1967. *Astrococcus* sect. *Haematostemon* Muell. Arg., Linnaea 34: 157. 1865. TYPE: *Haematostemon coriaceus* (Baill.) Pax & Hoffm.

A genus of two species from rainforests in southern Venezuela and Guiana. The gynoecium is very similar to that of *Angostyles*, but the staminate flowers are quite different.

189. Astrococcus Bentham, Hook. J. Bot. Kew Gard. Misc. 6: 327. 1854; Muell. Arg., DC. Prodr. 15(2): 766. 1866; Fl. Bras. 11(2): 330. 1874; Bentham, Gen. Pl. 3: 326. 1880; Pax & Hoffm., Pflanzenr. 147. IX (Heft 68): 30. 1919. TYPE: *Astrococcus cornutus* Benth.

A monotypic genus from Amazonian Brazil and Venezuela.

190. Angostyles Bentham, Hook. J. Bot. Kew Gard. Misc. 6: 328. 1854; Muell. Arg., DC. Prodr. 15(2): 767. 1866; Fl. Bras. 11(2): 331, t. 50. 1874; Bentham, Gen. Pl. 3: 327. 1880; Pax & Hoffm., Pflanzenr. 147. IX (Heft 68): 29. 1919. TYPE: *Angostyles longifolia* Benth.

A monotypic genus from the Brazilian Amazon.

191. Romanoa Trevisan, Saggio Monogr. Alghe Cocc. 99. 1848 (nom. cons.); Radcliffe-Smith, Kew Bull. 34: 589. 1980. *Anabaena* A. Juss., Euphorb. Tent. 46. 1824. *Anabaenella* Pax & Hoffm., Pflanzenr. 147. IX (Heft 68): 27. 1919. TYPE: *Anabaena tamnoides* A. Juss. [= *Romanoa tamnoides* (A. Juss.) Radcl.-Sm.].

A monotypic genus of Brazil, also very close to *Plukenetia* and questionably distinct.

192. Eleutherostigma Pax & Hoffmann, Pflanzenr. 147. IX (Heft 68): 11. 1919. TYPE: *Eleutherostigma lehmannianum* Pax & Hoffm.

A poorly known monotypic genus of Colombia and Ecuador, apparently closely related to *Plukenetia*, and combined with it by Gillespie (1993).

193. Plukenetia L., Sp. Pl. 1192. 1753; Gen. Pl. ed. 5, 438. 1754; Muell. Arg., DC. Prodr. 15(2): 768. 1866; Bentham, Gen. Pl. 3: 327. 1880; Pax & Hoffm., Pflanzenr. 147. IX (Heft 68): 12. 1919; Jablonski, Mem. New York Bot. Gard. 17: 142. 1967; Webster, Ann. Missouri Bot. Gard. 54: 293. 1968; Huft, Ann. Missouri Bot. Gard. 75: 1105. 1989; Gillespie, Syst. Bot. 18: 575. 1993. TYPE: *Plukenetia volubilis* L.

Pterococcus Hasskarl, Flora 25(2), Beibl. 41. 1842 (nom. cons.); Croizat, J. Arnold Arbor. 22: 423. 1941; Airy Shaw, Kew Bull. Add. Ser. 4: 187. 1975.
Ceratococcus Meissner, Pl. Vasc. Gen. 2: 369. 1843.
Sajorium Endl., Gen. Pl. Suppl. 3: 98. 1843. TYPE: *Pterococcus glaberrimus* Hassk., nom. illeg. [= *Plukenetia corniculata* J. E. Smith].
Hedraiostylus Hasskarl, Tijdschr. Natuurl. Gesch. Physiol. 10: 141. 1843. TYPE: *Hedraiostylus glaberrimus* (Hassk.) Hassk. [= *Plukenetia corniculata* J. E. Smith].
Tetracarpidium Pax, Bot. Jahrb. 26: 329. 1899. TYPE: *Tetracarpidium staudtii* Pax [= *Plukenetia conophora* Muell. Arg.].
Pseudotragia Pax, Bull. Herb. Boiss. II. 8: 635. 1908. TYPE: *Pseudotragia scandens* Pax [= *Plukenetia corniculata* J. E. Sm.].
Angostylidium Pax & Hoffm., Pflanzenr. 147. IX (Heft 68): 17. 1919. TYPE: *Angostylidium conophorum* (Muell. Arg.) Pax & Hoffm. [= *Plukenetia conophora* Muell. Arg.].
Apodandra Pax & Hoffm., Pflanzenr. 147. IX (Heft 68): 20. 1919. TYPE: *Apodandra loretensis* (Ule) Pax & Hoffm. [= *Plukenetia loretensis* Ule].
Elaeophora Ducke, Ann. Jard. Bot. Rio Jan. 4: 112. 1925. TYPE: *Elaeophora abutaefolia* Ducke [= *Plukenetia abutifolia* (Ducke) Pax & Hoffm.].

A genus of about 15 species, mostly neotropical, but with three species in Africa, one in Madagascar, and one in southeast Asia. The genus is rather variable, and a number of workers have accepted either *Pterococcus* or *Tetracarpidium* as distinct genera. However, the present conservative concept may not be broad enough, since some of the other genera of subtribe Plukenetiinae listed here (e.g., *Vigia* and *Romanoa*) are only questionably distinct from *Plukenetia*.

194. Vigia Vellozo, Fl. Flum. 9: t. 127. 1832. TYPE: *Vigia serrata* Vell.

Fragariopsis St. Hilaire, Leçons Morph. Veg. 426. 1840. TYPE: *Fragariopsis scandens* St. Hil. [= *Vigia serrata* Vell.].
Accia St. Hilaire, Leçons Morph. Veg. 499. 1840. TYPE: *Accia scandens* St. Hil. [= *Vigia serrata* Vell.].
Botryanthe Klotzsch, Arch. Naturgesch. 7(1): 190. 1841. TYPE: *Botryanthe discolor* K. [= *Vigia serrata* Vell.].

A South American genus, probably monotypic, although Pax & Hoffmann (1931) recognized a second species, *Fragariopsis paxii* Pitt. Even though the name *Fragariopsis* has been universally used for this segregate from *Plukenetia* since the treatment of Baillon (1858), the name *Vigia* of Vellozo clearly has priority. Although the plate of Vellozo is crude, it represents publication as valid as the casual mention of *Fragariopsis* by St. Hilaire in his textbook. There seems no good reason to propose the name *Fragariopsis* for conservation, especially since it is only dubiously distinct from *Plukenetia*.

Subtribe 31b. TRAGIINAE Webster, Taxon 24: 598. 1975. TYPE: *Tragia* L.

Shrubs or herbs, often twining; indumentum of simple and stinging hairs; leaves simple to distinctly lobed, entire or dentate, without embedded laminar glands, not stipellate; inflorescences axillary or terminal and opposite leaves; stamens (2)3–50, filaments free or connate; pollen grains subglobose to suboblate, 3-colpate, 3-porate, or inaperturate, sexine intectate-baculate, semitectate-reticulate, or tectate-perforate; ovary 3-locular; styles nearly free to distinctly connate; fruit capsular.

As here delimited, the subtribe includes 8 genera with ca. 150 species; besides the widespread *Tragia*, there are 5 Old World and only 2 neotropical genera.

KEY TO THE GENERA OF SUBTRIBE TRAGIINAE

1a. Staminate sepals adaxially inflexed to form a pseudodisk; stamens 3 or 4, anthers introrse; styles massive.
  2a. Pistillate sepals entire or toothed; pistillode absent in staminate flower.
    3a. Pistillate sepals entire; anther connective enlarged, triangular, sometimes caudate; stamens free.
      4a. Styles free or nearly so, long-papillose on adaxial surface; inflorescence terminal and leaf-opposed; leaves with stinging hairs ..... 195. *Cnesmone*
      4b. Styles connate into a massive globose or clavate column, not papillose; inflorescence axillary; leaves subglabrous ... 196. *Megistostigma*
    3b. Pistillate sepals toothed; anther connective not enlarged or caudate; stamens connate at base; styles connate, column globose; inflorescence terminal and leaf-opposed; leaves subglabrous ..... 197. *Sphaerostylis*
  2b. Pistillate sepals distinctly pinnatifid; pistillode present in staminate flower; leaves with stinging hairs ..... 198. *Tragiella*
1b. Staminate sepals not adaxially inflexed; stamens 2 to many, anthers introrse or extrorse; styles usually slender.
  5a. Anthers 3 or more, if 2 then not subsessile; staminate calyx concave; styles free to partly connate.
    6a. Anther connective without tuft of stinging hairs; stamens (2)3–many; subshrubs, herbs, or twining vines, usually monoecious.
      7a. Styles thick, papillose; staminal receptacle convex; stamens 4–18 ..... 199. *Platygyna*
      7b. Styles slender, not papillose; staminal receptacle plane; stamens 2–8(–50) ..... 200. *Tragia*
    6b. Anther connective ending in tuft of stinging hairs; erect shrubs, leaves glabrescent, dioecious ..... 201. *Acidoton*
  5b. Anthers 2, subsessile; staminate calyx flat with lobes reflexed; styles connate into a thick column ..... 202. *Pachystylidium*

195. Cnesmone Blume, Bijdr. Fl. Ned. Ind. 630. 1826 (as *Cnesmosa*); Fl. Javae vi. 1828; Muell. Arg., DC. Prodr. 15(2): 926. 1866; Bentham, Gen. Pl. 3: 330. 1880; Hook. f., Fl. Brit. Ind. 5: 466. 1888; J. J. Smith, Med. Dept. Landbouw 10: 513. 1910; Pax & Hoffm., Pflanzenr. 147. IX (Heft 68): 102. 1919; Croizat, J. Arnold Arbor. 22: 427. 1941; Airy Shaw, Kew Bull. 26: 240. 1972; Balakrisnan & Nair, Gardener's Bull. 31: 49. 1978. TYPE: *Cnesmone javanica* Bl.

Cenesmon Gagnep., Bull. Soc. Bot. France 71: 866. 1924; Fl. Gen. Indochine 5: 386. 1926. TYPE: *Cenesmon tonkinense* Gagnep. [= *Cnesmone tonkinense* (Gagnep.) Croizat; lectotype, designated by Wheeler, Taxon 24: 534. 1975].

This Asian genus of ca. ten species is here delimited following Croizat (1941).

196. Megistostigma Hooker f., Hook. Ic. Pl. 16: t. 1592. 1887; Fl. Brit. Ind. 5: 466. 1888; Merrill, Phil. J. Sci. 16C: 563. 1920; Croizat, J. Arnold Arbor. 22: 425. 1941; Airy Shaw, Kew Bull. 23: 119. 1969. TYPE: *Megistostigma malaccense* Hook. f.

Clavistylus J. J. Smith, Med. Dept. Landb. 10: 517. 1910. TYPE: *Clavistylus peltatus* J. J. Sm. [= *Megistostigma peltatum* (J. J. Sm.) Croizat].

A tropical southeast Asian genus of five species distributed from Burma to China, the Philippines, and Borneo; combined with *Sphaerostylis* by Pax & Hoffmann (1919) but maintained as distinct by Croizat (1941).

197. Sphaerostylis Baillon, Etude Gén. Euphorb. 466. 1858; Muell. Arg., DC. Prodr. 15(2): 768. 1866; Bentham, Gen. Pl. 3: 327. 1880; Baillon, Hist. Phys. Nat. Madag. 4(29): t. 196. 1891; Pax & Hoffm., Pflanzenr. 147. IX (Heft 68): 106. 1919; Croizat, J. Arnold Arbor. 22: 430. 1941. TYPE: *Sphaerostylis tulasneana* Baill.

A genus of two species endemic to Madagascar.

198. Tragiella Pax & Hoffmann, Pflanzenr. 147. IX (Heft 68): 104. 1919; Radcliffe-Smith, Kew Bull. 35: 777. 1981; Fl. E. Trop. Afr. Euphorb. 1: 318. 1987. TYPE: *Tragiella natalensis* (Sond.) Pax & Hoffm. [lectotype, chosen here].

An African genus of five species, extremely close to *Sphaerostylis* and doubtfully separable.

199. Platygyna Mercier, Bull. Bot. (Seringe) 1: 168. 1830; Muell. Arg., DC. Prodr. 15(2): 913. 1866 (as *Platygyne*); Bentham, Gen. Pl. 3: 328. 1880; Pax & Hoffm., Pflanzenr. 147. IX (Heft 68): 26. 1919; Alain, Fl. Cuba 3: 100. 1953; Mem. New York Bot. Gard. 21: 132. 1971; Borhidi, Ann. Hist.-Nat. Mus. Nat. Hung. 64: 89. 1972. TYPE: *Platygyna urens* Merc. [= *Platygyna hexandra* (Jacq.) Muell. Arg.].

Acanthocaulon Klotzsch ex Endl., Gen. Pl. Suppl. 4(3): 88. 1850. TYPE: *Acanthocaulon pruriens* Kl. ex Endl. [= *Platygyna hexandra* (Jacq.) Muell. Arg.].

In the most recent revision of Borhidi (1972), *Platygyna* is a genus of seven species endemic to Cuba. Alain (1971) reduced *Platygyna* to a synonym of *Tragia*, a disposition that merits further study.

200. Tragia Plumier ex L., Sp. Pl. 980. 1753; Gen. Pl. ed. 5, 421. 1754; Muell. Arg., DC. Prodr. 15(2): 927. 1866; Bentham, Gen. Pl. 3: 329. 1880; Prain, Fl. Trop. Afr. 6(1): 964. 1913; Pax & Hoffm., Pflanzenr. 147. IX (Heft 68): 32. 1919; Prain, Fl. Capensis 5(2): 502. 1920; Lourteig & O'Donell, Lilloa 6: 347. 1941; Johnston, Rhodora 64: 137. 1962; Miller & Webster, Rhodora 69: 241. 1967; Webster, J. Arnold Arbor. 48: 376. 1967; Leandri, Adansonia II. 11: 437. 1971; Radcliffe-Smith, Fl. E. Trop. Afr. Euphorb. 1: 291. 1987; Webster & Huft, Ann. Missouri Bot. Gard. 75: 1106. 1989. TYPE: *Tragia volubilis* L. [lectotype, designated by Small, in Britton & Brown, Ill. Fl. N. U.S., ed. 2, 2: 458. 1913].

Bia Klotzsch, Arch. Naturgesch. 7(1): 189. 1841. TYPE: *Bia alienata* Didr. [= *Tragia alienata* (Didr.) Múlg. & M. Guttiérrez, Candollea 46: 523. 1991; this name unfortunately must replace *Tragia sellowiana* Muell. Arg., 1866; lectotype].

Leptorhachis Klotzsch, Arch. Naturgesch. 7(1): 189. 1841. TYPE: *Leptorhachis hastata* Kl. [= *Tragia hastata* (Kl.) Muell. Arg.].

Leucandra Klotzsch, Arch. Naturgesch. 7(1): 188. 1841. TYPE: *Leucandra betonicaefolia* Kl. [= *Tragia leucandra* Pax & Hoffm.].

Ctenomeria Harvey, Hook. London J. Bot. 1: 29. 1842. TYPE: *Ctenomeria cordata* Harv. [= *Tragia capensis* Thunb.].

Lassia Baillon, Etude Gén. Euphorb. 464. 1858. TYPE: *Lassia scandens* Baill. [= *Tragia scandens* (Baill.) Muell. Arg.].

Zuckertia Baillon, Etude Gén. Euphorb. 495. 1858. TYPE: *Zuckertia cordata* Baill. [= *Tragia bailloniana* Muell. Arg.].

A large and diverse genus of ca. 125 species, mainly in Africa and America. The genus is palynologically heterogeneous, and some taxa such as *Zuckertia* may prove to merit segregation on further study.

201. Acidoton Swartz, Prodr. 6, 83. 1788 (nom. cons.); Fl. Ind. Occ. 2: 952, t. 18. 1800; Muell. Arg., DC. Prodr. 15(2): 914. 1866; Bentham, Gen. Pl. 3: 328. 1880; Urban, Symb. Ant. 7: 513. 1913; Pax & Hoffm., Pflanzenr. 147. IX (Heft 68): 24. 1919; Fawc. & Rend., Fl. Jam. 4: 303. 1920; Webster, Ann. Missouri Bot. Gard. 54: 191. 1967; 54: 289. 1968; Liogier, Fl. Española 4: 71. 1986. TYPE: *Acidoton urens* Sw.

Gitara Pax & Hoffm., Pflanzenr. 147. XVII (Heft 85): 187. 1924. TYPE: *Gitara venezolana* Pax & Hoffm. [= *Acidoton nicaraguensis* (Hemsl.) Webster].

A neotropical genus of six or seven species, in the Greater Antilles (Jamaica and Hispaniola), southern Central America, and northern South America.

202. Pachystylidium Pax & Hoffmann, Pflanzenr. 147. IX (Heft 68): 108. 1919; Backer & Bakh., Fl. Java 1 : 491. 1963; Airy Shaw, Kew Bull. 23: 115. 1969. TYPE: *Pachystylidium hirsutum* (Bl.) Pax & Hoffm. [*Tragia hirsuta* Bl.].

A monotypic genus of tropical Asia (India to Indochina, Java, and the Philippines; not reported from Sumatra or Borneo).

Subtribe 31c. DALECHAMPIINAE (Muell. Arg.) Webster, stat. nov. Tribe Dalechampieae Muell. Arg., Bot. Zeit. 22: 324. 1864; DC. Prodr. 15(2): 1232. 1866. TYPE: *Dalechampia* Plum. ex L.

Monoecious undershrubs or more often clambering or twining; indumentum of simple and stinging hairs (sometimes almost absent); leaves alternate, blades simple, lobed or partite, usually stipellate; stipules persistent; inflorescences pseudanthial, subtended by a pair of usually showy involucral bracts; pistillate flowers 3 per pseudanthium, in a basal cymule; staminate pleiochasium terminal, with mostly 8–12 flowers; staminate bractlets mostly resiniferous; stamens 8 100 or more, filaments connate; pollen grains prolate, 3-colporate, sexine with prominent raised reticulum; pistillode absent; pistillate sepals entire to pinnatifid; ovary 3-locular; stylar column elongated, stigmatic surface extending down upper ⅓ to ¾; fruit capsular.

This subtribe contains only the single genus *Dalechampia*. Although it has been treated at tribal rank by almost all workers since Mueller (1866), *Dalechampia* has links to both the Tragiinae (stinging hairs) and Plukenetiinae (elongate stylar column).

203. Dalechampia Plumier ex L., Sp. Pl. 1054. 1753; Gen. Pl. ed. 5, 473. 1754; Muell, Arg.,

DC. Prodr. 15(2): 1232. 1866; Fl. Bras. 11(2): 633. 1874; Bentham, Gen. Pl. 3: 330. 1880; Pax & Hoffm., Pflanzenr. 147. XII (Heft 68): 3. 1919; Léonard, Fl. Congo Rwanda-Burundi 8(1): 194. 1962; Jablonski, Mem. New York Bot. Gard. 17: 145. 1967; Webster, Ann. Missouri Bot. Gard. 54: 308. 1968; Webster & Armbruster, Brittonia 31: 352. 1979; Syst. Bot. 7: 484. 1982; Armbruster, Syst. Bot. 9: 272. 1984; Radcliffe-Smith, Fl. E. Trop. Afr. Euphorb. 1: 285. 1987; Armbruster, Syst. Bot. 13: 303. 1988; Webster, Ann. Missouri Bot. Gard. 75: 1108. 1988; Armbruster, Brittonia 41: 44. 1989; Webster, Brittonia 41: 1. 1989; Webster & Armbruster, Bot. J. Linn. Soc. 105: 137. 1991. TYPE: *Dalechampia scandens* L.

Cremophyllum Scheidweiler, Bull. Acad. Roy. Sci. Brux. 9(1): 23. 1842. TYPE: *Cremophyllum spathulatum* Scheidw. [= *Dalechampia spathulata* (Scheidw.) Baillon].

Megalostylis Spencer Moore, J. Bot. 54: 208. 1916. TYPE: *Megalostylis poeppigii* Sp. Moore [= *Dalechampia micrantha* Poepp.].

A genus of slightly over 100 species, about 90 of which are American, with a few in Africa, Madagascar, and India, and a single species reaching southern China and Java. The genus is diverse, and Webster & Armbruster (1991) have recognized 6 sections for the 90-odd neotropical species.

Tribe 32. OMPHALEAE (Pax & Hoffmann) Webster, Taxon 24: 598. 1975. Hippomaneae subtribe Omphaleinae Pax & Hoffm., Pflanzenr. 147. IV (Heft 52): 14. 1912. TYPE: *Omphalea* L.

Monoecious trees, shrubs, or lianas; stems with reddish latex; indumentum simple; leaves alternate, simple or lobed, pinnately or palmately veined, usually with 2 sessile basal glands; stipules deciduous. Inflorescences terminal or axillary, paniculate, bracts ± foliose and biglandular; flowers apetalous. Staminate sepals 4 or 5, decussate or imbricate; disk annular or lobed, often massive; stamens 2 or 3, filaments connate, anther connectives free or fused; pollen grains oblate, 3-colporate, sexine finely punctate-spinulose; pistillode absent. Pistillate sepals 4 or 5, imbricate; disk tenuous or obsolete; ovary 3-locular; styles connate into a stout column, stigmas undivided. Fruit thick-walled, capsular or indehiscent; seeds large, globose, ecarunculate, testa dry; endosperm copious.

This tribe contains the single genus *Omphalea*, whose affinities have been controversial for many years. Early workers, such as A. Jussieu (1824) and Baillon (1858), associated it with the Hippomaneae. Mueller (1866) kept it in the tribe Hippomaneae, in subtribe Gelonieae. Pax & Hoffmann (1912) created a special subtribe of Hippomaneae for *Omphalea*, but later (1931) abandoned their subtribe and inserted the genus in the Gelonieae. Croizat (1942), in contrast, pointed out affinities with the tribe Plukenetieae, and Punt (1962) noted that pollen morphology supports Croizat's opinion.

Although *Omphalea* shows striking resemblances to the Plukenetieae in a number of characters, it also approaches the tribe Stomatocalyceae, and thus provides a link between subfamilies Acalyphoideae and Euphorbioideae. Clarification of its affinities appears to be critical in establishing the phylogeny of the uniovulate Euphorbiaceae.

204. Omphalea L., Syst. Nat. ed. 10, 1264. 1759 (nom. cons.); Muell. Arg., DC. Prodr. 15(2): 1134. 1866; Bentham, Gen. Pl. 3: 332. 1880; Pax & Hoffm., Pflanzenr. 147. V (Heft 52): 14. 1912; Fawc. & Rend., Fl. Jam. 4: 319. 1920; Croizat, Bull. Jard. Bot. Buit. III. 17: 204. 1941; Alain, Fl. Cuba 3: 109. 1953; Webster, Ann. Missouri Bot. Gard. 54: 295. 1968; Airy Shaw, Kew Bull. 23: 130. 1969; Alain, Mem. New York Bot. Gard. 21(2): 124. 1971; Airy Shaw, Kew Bull. Add. Ser. 8: 177. 1980; Liogier, Fl. Española 4: 178. 1986; Radcliffe-Smith, Fl. E. Trop. Afr. Euphorb. 1: 371. 1987; Gillespie, Rev. Phyl. Anal. *Omphalea* 144 (dissert.). 1988. *Omphalandria* P. Browne, Civ. Nat. Hist. Jamaica 334. 1756 (nom. rej.). *Duchola* Adanson, Fam. Pl. 2: 357. 1763 (nom. superfl.). TYPE: *Omphalea triandra* L. (typ. cons.).

Ronnowia Buchoz, Pl. Nouv. Decouv. 6, t. 4. 1779. TYPE: *Ronnowia domingensis* Buchoz (nom. illeg.) [= *Omphalea triandra* L.].

Hecatea Thouars, Hist. Pl. Iles Afrique Austr. 27, t. 5. 1804. TYPE: *Hecatea oppositifolia* Willd. [= *Omphalea oppositifolia* (Willd.) Gillespie; lectotype, designated by Gillespie].

Hebecocca Beurling, Kongl. Vetensk. Akad. Handl. 1854: 146. 1856. TYPE: *Hebecocca panamensis* Beurl. [= *Omphalea diandra* L.].

Neomphalea Pax & Hoffm., Pflanzenr. 147. XIV (Heft 68): 54. 1919. TYPE: *Neomphalea papuana* (Pax & Hoffm.) Pax & Hoffm. [= *Omphalea papuana* Pax & Hoffm.].

A genus of ca. 15 species in both the Old World and New World, but with the greatest species concentrations in the Greater Antilles and Madagascar

Subfamily IV. CROTONOIDEAE Pax, Bot. Jahrb. 5: 413. 1884; Natürl. Pflanzenfam. ed. 1, 3(5): 14. 1890. TYPE: *Croton* L.

Trees, shrubs, or herbs; latex colored or absent; indumentum simple, stellate, or lepidote; leaves alternate, opposite, or rarely whorled, stipulate or exstipulate; blade simple or palmately lobed or compound, often with foliar glands. Inflorescences axillary or terminal, dichasial to racemose or spicate. Staminate flower: sepals imbricate or valvate; petals and disk present or absent; stamens (3–)5–many, filaments free or connate; pollen grains binucleate or trinucleate, tricolporate to more commonly porate or inaperturate, sexine mostly with ornamentation of knobs in hexagonal pattern; pistillode present or absent. Pistillate flower: sepals (2)3–6, imbricate or valvate, often connate; petals and disk present or absent; ovary mostly 2–4-locular; styles bifid to multifid (rarely entire); ovules solitary in each locule, anatropous. Fruit capsular (rarely indehiscent); seeds carunculate or ecarunculate, testa sometimes fleshy; endosperm usually copious, often oily.

As defined here, following Webster (1975), subfamily Crotonoideae includes 12 tribes. This is a much narrower circumscription than that of Pax (1890), which took in nearly all of the uniovulate taxa of Euphorbiaceae. It is considerably broader than the subfamily Crotonoideae of Hurusawa (1954), which included only the tribe Crotoneae.

In the classic system of Mueller (1866), genera of the presently accepted Crotonoideae were dispersed between tribes Crotoneae, Acalypheae, and Hippomaneae. Bentham (1880) placed many of the Crotonoideae in the first two subtribes of his tribe Crotoneae, but in other subtribes had a mixture of Acalyphoideae and Crotonoideae. Hutchinson (1969) placed many Crotonoideae in his tribes 13–20, 38, and 39; but 5 of those tribes also included genera of either Acalyphoideae or Euphorbioideae.

As predicted by Erdtman (1952), pollen morphology has provided decisive evidence in establishing lines of phylogenetic affinity within the Crotonoideae. Punt (1962), following Erdtman's lead, grouped most of the genera of Crotonoideae under his "*Croton* configuration." However, "crotonoid" pollen is useful mainly for establishing membership in the subfamily, and except in the more primitive tribes does not help to clarify problems of tribal delimitation.

KEY TO THE TRIBES OF SUBFAMILY CROTONOIDEAE

1a. Pollen grains colporate or porate, sexine reticulate to clavate; petals absent; indumentum mostly simple.
  2a. Laticifers articulated; pollen grains 3-nucleate; plants mostly monoecious; basic chromosome number $x = 9$.
    3a. Pollen grains colporate; styles bifid; seeds carunculate or ecarunculate; endosperm oily ..... 33. MICRANDREAE
    3b. Pollen grains periporate; styles mostly multifid; seeds carunculate; endosperm starchy ..... 34. MANIHOTEAE
  2b. Laticifers nonarticulated; pollen grains 2-nucleate; plants mostly dioecious; basic chromosome number $x = 11$.
    4a. Pollen grains colporate; leaves non-pellucid-punctate, stipules free; inflorescences axillary, mostly spicate or paniculate ..... 35. ADENOCLINEAE
    4b. Pollen grains periporate; leaves pellucid-punctate, stipules connate; flowers in clusters opposite the leaves ..... 36. GELONIEAE
1b. Pollen grains inaperturate, sexine with "crotonoid" pattern; petals usually present; indumentum simple, malpighiaceous, or stellate; laticifers nonarticulate (except in some Jatropheae).
  5a. Seeds without endosperm, cotyledons massive; inflorescences dichasial; petals absent; styles undivided, dilated; latex milky ..... 37. ELATERIOSPERMEAE
  5b. Seeds with copious endosperm, cotyledons thin; petals present at least in staminate flowers (except in Neoboutonieae); inflorescences various; styles bifid to multifid, less commonly unlobed.
    6a. Staminate sepals imbricate, free or if connate then not completely covering petals in the bud; seeds carunculate or ecarunculate.
      7a. Indumentum simple.
        8a. Stamens mostly more than 5, free or connate; pollen sexine coarsely clavate.
          9a. Inflorescences terminal, mostly dichasial; leaves mostly palmately lobed or compound; fruits capsular or drupaceous, seeds carunculate or ecarunculate ..... 38. JATROPHEAE
          9b. Inflorescences terminal or axillary, racemose or spicate to paniculate; leaves unlobed, usually without basal glands; fruit capsular ..... 39. CODIAEAE
        8b. Stamens 3–5, filaments connate; pollen sexine finely clavate; monoecious; inflorescences terminal or axillary, racemose or thyrsoid; seeds ecarunculate ..... 40. TRIGONOSTEMONEAE
      7b. Indumentum (at least in part) of stellate or lepidote hairs.

10a. Fruit capsular, seeds ecarunculate; petals free or absent.
11a. Pollen sexine with spinose or reduced processes; leaves exstipulate; filaments often connate, at least in part; cotyledons broad or narrow ..... 41. RICINOCARPEAE
11b. Pollen sexinous, processes not spinose or reduced; leaves usually stipulate; filaments free; cotyledons broad ..... 42. CROTONEAE
10b. Fruit drupaceous, seeds ecarunculate; petals ± coherent ..... 43. RICINODENDREAE
6b. Staminate sepals fused in the bud, splitting valvately or irregularly into segments; fruit capsular or drupaceous; seeds ecarunculate ..... 44. ALEURITIDEAE

Tribe 33. MICRANDREAE (Muell. Arg.) Webster, Taxon 24: 598. 1975. Crotoneae subtribe Micrandreae Muell. Arg., DC. Prodr. 15(2): 709. 1866. Gelonieae subtribe Chaetocarpinae series Micrandriformes Pax & Hoffm., Pflanzenr. 147. XIV (Heft 68): 49. 1919. TYPE: *Micrandra* Benth.

Monoecious or dioecious trees; stems with articulate laticifers and usually whitish latex; indumentum simple or stellate; leaves alternate, unlobed, entire, pinnately veined or triplinerved, with laminar glands at apex of petiole; stipules often caducous. Inflorescences terminal or axillary, dichasial-paniculate, bracts small or large; flowers apetalous. Staminate sepals 5, imbricate, free or connate; disk dissected, lobed, or absent; stamens 5–10, free or connate; pollen grains 3-nucleate, 3-colporate, colpi operculate, sexine reticulate; pistillode present or absent. Pistillate sepals 5, imbricate, free, deciduous in fruit; disk 5-lobed; ovary 3-locular; styles free, bifid. Fruit capsular; columella persistent; seeds large, carunculate or ecarunculate, endosperm oily.

As treated by Webster (1975), the tribe includes three or four genera distributed into two subtribes. The Micrandreae clearly form a link between subfamilies Acalyphoideae and Crotonoideae.

KEY TO THE SUBTRIBES OF TRIBE MICRANDREAE

1a. Leaves simple; stamens free, sometimes inflexed in bud; sepals discrete, imbricate or valvate ..... 33a. Micrandrinae
1b. Leaves palmately compound; stamens connate; sepals connate, valvate ..... 33b. Heveinae

Subtribe 33a. MICRANDRINAE Muell. Arg., DC. Prodr. 15(2): 709. 1866. TYPE: *Micrandra* Benth.

Leaves simple, unlobed. Panicles with bracts conspicuous or inconspicuous. Staminate sepals imbricate, free or nearly so; disk dissected; stamens 5–7, filaments free, ± inflexed in bud; pistillode present; pistillate disk annular.

A subtribe of three South American genera.

KEY TO THE GENERA OF SUBTRIBE MICRANDRINAE

1a. Sepals free; staminate disk present; stamens 5–8; floral bracts small.
2a. Anthers elliptical; indumentum simple ..... 205. *Micrandra*
2b. Anthers linear; indumentum stellate ..... 206. *Micrandropsis*
1b. Sepals connate; staminate disk absent; stamens 8–10; floral bracts large ..... 207. *Cunuria*

205. Micrandra Bentham, Hook. Kew J. Bot. 6: 371. 1854 (nom. cons.); Muell. Arg., DC. Prodr. 15(2): 709. 1866; Fl. Bras. 11(2): 289. 1873; Bentham, Gen. Pl. 3: 289. 1880; Pax, Pflanzenr. 147. I (Heft 42): 18. 1910; Schultes, Bot. Mus. Leafl. 15: 201. 1952. TYPE: *Micrandra siphonioides* Benth. (typ. cons.).

Pogonophyllum Didr., Vidensk. Medd. Dansk Naturh. Foren. Kjøbenhaven 1857: 144. 1857. TYPE: *Pogonophyllum elatum* Didr. [= *Micrandra elata* (Didr.) Muell. Arg.].

A poorly understood genus of about seven Amazonian species.

206. Micrandropsis Rodrigues, Acta Amazonica 3(2): 5. 1973. TYPE: *Micrandropsis scleroxylon* (W. Rodr.) W. Rodr.

A monotypic genus of Amazonian Brazil.

207. Cunuria Baillon, Adansonia I. 4: 287. Aug. 1864; Muell. Arg., DC. Prodr. 15(2): 1123. 1866; Bentham, Gen. Pl. 3: 289. 1880; Pax, Pflanzenr. 147. I (Heft 42): 16. 1910; Baldwin & Schultes, Bot. Mus. Leafl. Harvard Univ. 12: 325. 1947. TYPE: *Cunuria spruceana* Baillon.

Clusiophyllum Muell. Arg., Flora 47: 518. 25 Oct. 1864. TYPE: *Clusiophyllum sprucei* Muell. Arg. [= *Cunuria crassipes* Muell. Arg.].

Baldwin & Schultes (1947) recognized five species of *Cunuria*, all from Amazonian South America. Schultes (1952) on reconsideration reduced *Cunuria* to a synonym of *Micrandra*, and because of his intimate knowledge of these South American

trees his opinion must be weighted heavily. The listing of *Cunuria* as a separate genus is done here mainly to call attention to the problem, not to affirm its generic distinctness.

Subtribe 33b. HEVEINAE Muell. Arg., Linnaea 34: 202. 1865; DC. Prodr. 15(2): 716. 1866. TYPE: *Hevea* Aubl.

Leaves palmately compound. Panicles with inconspicuous bracts. Staminate sepals connate into a cup, lobes valvate; disk lobed or dissected; stamens 5–10, filaments connate into a column, anthers sessile; pistillode present; pistillate disk dissected or obsolete; seeds ecarunculate.

As originally delimited by Mueller (1865, 1866), subtribe Heveinae is here interpreted to include the single genus *Hevea*. Pax (1910) placed *Hevea* in subtribe Jatrophinae, a disposition that is contradicted by pollen morphology, chromosome number, and other characters.

208. Hevea Aublet, Hist. Pl. Guiane Fr. 2: 871, t. 335. 1775; Muell. Arg., DC. Prodr. 15(2): 716. 1866; Fl. Brasil. 11(2): 297. 1874; Pax, Pflanzenr. 147. I. (Heft 42): 117. 1910; Ducke, Arch. Inst. Biol. Veg. Rio Janeiro 2: 217. 1935; Schultes, Bot. Mus. Leafl. Harvard Univ. 12: 1. 1945; 13: 1. 1947; 14: 79. 1950; 15: 111, 247, 255. 1952; 16: 21. 1953; 25: 243. 1977; Bot. Review 36: 197. 1970; Econ. Bot. 41: 125. 1987; Malaysian Rubber Res. Dev. Board Mon. 14: 5. 1990. TYPE: *Hevea guianensis* Aubl.

Siphonia L. C. Richard, in Schreber, Gen. Pl. 2: 656. 1791. TYPE: *Siphonia elastica* Pers. [= *Hevea guianensis* Aubl.; lectotype].

Caoutchoua J. F. Gmelin, Syst. Nat. 2: 677. 1791. TYPE: *Caoutchoua elastica* Gmel. [= *Hevea guianensis* Aubl.].

According to Schultes (1990), *Hevea* includes ten species with several varieties, all found within Amazonian South America. Because of the economic importance of the genus, there is extensive literature on its systematics; references may be found in Schultes (1970, 1990).

Tribe 34. MANIHOTEAE (Muell. Arg.) Pax, Natürl. Pflanzenfam. ed. 1, 3(5): 77. 1890. Hippomaneae subtribe Manihoteae Muell. Arg., DC. Prodr. 15(2): 1056. 1866. TYPE: *Manihot* Miller.

Monoecious (rarely dioecious) trees, shrubs, or herbs; laticifers articulated, latex white; indumentum simple (stinging hairs sometimes present); leaves alternate, mostly palmately lobed or dissected; petioles glandular or stipellate at apex; stipules usually present. Inflorescences terminal or pseudoaxillary, most racemose-paniculate or dichasial-paniculate, usually bisexual; flowers apetalous. Staminate flower: calyx synsepalous, sepals 5, imbricate, ± petaloid; disk intrastaminal or extrastaminal; stamens 8–10(–25), filaments free or connate; pollen grains globose, 3-nucleate, periporate, sexine with Croton-pattern; pistillode present or absent. Pistillate flower: sepals 5, free or connate, sometimes deciduous; disk annular, sometimes with staminodia; ovary 3-locular (rarely 5-locular); styles free, mostly multifid or lacerate (rarely bifid). Fruit capsular; columella often persistent; seeds carunculate, testa dry.

As delimited here, tribe Manihoteae includes two genera, both confined to the New World. The close affinity between *Manihot* and *Cnidoscolus* was independently confirmed on palynological grounds by Punt (1962) and Miller & Webster (1962).

KEY TO THE GENERA OF TRIBE MANIHOTEAE

1a. Stinging hairs absent; stamens free, staminate disk intrastaminal; staminate perianth usually yellowish or greenish; leaf blades stipellate (not glandular) at base; inflorescence racemose or racemose-paniculate ..... 209. *Manihot*

1b. Stinging hairs present; stamens connate (very rarely free); staminate disk extrastaminal, annular; staminate perianth whitish; leaf blades glandular (not stipellate) at base; inflorescence dichasial-paniculate ..... 210. *Cnidoscolus*

209. Manihot Miller, Gard. Dict. ed. 4. 1754; Pohl, Pl. Bras. Ic. 1: 17. 1827; Muell. Arg., DC. Prodr. 15(2): 1057. 1866; Bentham, Gen. Pl. 3: 306. 1880; Pax, Pflanzenr. 147. II (Heft 44): 21. 1910; Croizat, J. Arnold Arbor. 23: 216. 1942; Rogers & Appan, Fl. Neotrop. 13: 1. 1973; Rogers & Fleming, Econ. Bot. 27: 1. 1973; Allem, Rev. Brasil. Biol. 49: 1–26. 1989. *Mandioca* Link, Handb. 2: 436. 1831. TYPE: *Manihot esculenta* Crantz [*Jatropha manihot* L.].

Janipha HBK, Nov. Gen. Sp. 2: 106, t. 109. 1817. TYPE: *Janipha aesculifolia* HBK [= *Manihot aesculifolia* (HBK) Pohl].

Manihotoides Rogers & Appan, Fl. Neotrop. 13: 247. 1973. TYPE: *Manihotoides pauciflora* (Bdge.) Rogers & Appan [= *Manihot pauciflora* Bdge.].

A neotropical genus of ca. 60 species, mostly native to Brazil. Rogers & Appan (1973) created a new genus, *Manihotoides*, for an aberrant spe-

cies in Mexico characterized by reduced inflorescences, and trifoliolate leaves clustered on short shoots. However, the recent discovery of another Mexican species (ined.) with unlobed leaves on short shoots largely erases the supposed distinction.

210. Cnidoscolus Pohl, Pl. Bras. 1: 56. 1827; Pax & Hoffm., Natürl. Pflanzenfam. ed. 2, 19c: 1964. 1931; Lourteig & O'Donell, Lilloa 9: 105. 1943; McVaugh, Bull. Torrey Bot. Club 71: 457. 1944; Lundell, Bull. Torrey Bot. Club 72: 319. 1945; Webster, J. Arnold Arbor. 48: 349. 1967; Breckon, Brittonia 31: 125. 1979. TYPE: *Cnidoscolus hamosus* Pohl [lectotype, designated by Small, in Britton & Brown, Ill. Fl. N. U.S. ed. 2, 2: 462. 1913].

Jussieuia Houstoun, Reliq. Houst. 6. 1781 (non *Jussiaea* L., 1753). TYPE: *Jatropha herbacea* L. [= *Cnidoscolus herbaceus* (L.) I. M. Johnston].

Bivonea Raf., Specchio 1: 156. 1814 (nom. rej.). TYPE: *Bivonea stimulosa* (Michx.) Raf. [= *Cnidoscolus stimulosus* (Michx.) Engelm. & Gray].

Victorinia León, Mem. Soc. Cub. Hist. Nat. Felipe Poey 15: 242. 1941. TYPE: *Victorinia regina* (León) León [*Jatropha regina* León; = *Cnidoscolus regina* (León) McVaugh].

A neotropical genus of ca. 50 species, with the greatest concentration in Mexico. The genus was reviewed by McVaugh (1944), and his reduction of *Victorinia* to synonymy appears justified.

Tribe 35. ADENOCLINEAE (Muell. Arg.) Webster, Taxon 24: 598. 1975. Hippomaneae subtribe Adenoclineae Muell. Arg., Linnaea 34: 203. 1865; DC. Prodr. 15(2): 1139. 1866. TYPE: *Adenocline* Turcz.

Monoecious or dioecious trees, shrubs, or herbs; latex clear (± colored); indumentum simple, malpighiaceous, or stellate; leaves alternate (rarely opposite), simple, penninerved or triplinerved, with or without laminar or petiolar glands; stipules persistent or deciduous. Inflorescences terminal, axillary, or opposite the leaves, spicate to paniculate or glomerular; flowers apetalous. Staminate sepals 3–5, imbricate, free or connate; disk dissected or absent; stamens 3–30, filaments free or connate; pollen grains 2-nucleate, 3-colporate, colpi operculate or inoperculate, sexine with Croton-pattern; pistillode present or absent. Pistillate sepals 3–5, imbricate, free or connate; disk dissected or annular, sometimes staminodial; ovary 2–6-locular; styles bifid or stigmatiform. Fruit capsular or drupaceous; seeds ecarunculate, seed-coat dry or fleshy; endosperm present.

Most of the genera of this tribe were referred to the Gelonieae by Pax & Hoffmann (1931), but were scattered in different subtribes and associated with genera belonging to three different subfamilies. Following the arrangement of Webster (1975), the six genera are grouped into two subtribes.

KEY TO THE SUBTRIBES OF TRIBE ADENOCLINEAE

1a. Indumentum simple; stamens free; fruit dehiscent or indehiscent, 2–3-locular ..... 35a. Adenoclininae
1b. Indumentum stellate; stamens connate; fruit baccate, 1–7-locular ..... 35. Endosperminae

Subtribe 35a. ADENOCLININAE Muell. Arg., Linnaea 34: 203. 1865; DC. Prodr. 15(2): 1139. 1866. TYPE: *Adenocline* Turcz.

Gelonieae subtribe Tetrorchidiinae Pax, Pflanzenr. 147. IV (Heft 52): 29. 1912. TYPE: *Tetrorchidium* Poepp.

Trees, shrubs, or herbs; indumentum simple or malpighiaceous; inflorescence diverse; stamens 3–30, free; ovary 2- or 3-locular; stigmas distinct; fruit capsular or drupaceous.

This subtribe includes 5 genera with ca. 30 species of the Neotropics and Africa.

KEY TO THE GENERA OF SUBTRIBE ADENOCLININAE

1a. Pistillate disk present, at least as staminodia.
  2a. Stamens 25–30; fruits drupaceous; ovary 2-locular; leaves entire, with laminar glands ..... 211. *Glycydendron*
  2b. Stamens less than 20; fruits capsular; ovary 2–3-locular; leaves ± dentate, with or without laminar glands.
    3a. Trees or shrubs; seed-coat fleshy; staminate disk not of interstaminal processes.
      4a. Stamens 8–10; anthers 2-locular, not peltate; staminate disk present; leaves eglandular, stipules caducous; indumentum simple; endotesta smooth ..... 212. *Klaineanthus*
      4b. Stamens 3; anthers 4-locular, peltate; staminate disk absent; leaves usually with laminar glands, stipules persistent; indumentum malpighiaceous (at least in part); endotesta foveolate or echinulate ..... 213. *Tetrorchidium*
    3b. Herbs; seed-coat dry; staminate disk of interstaminal processes ..... 214. *Adenocline*
1b. Pistillate disk absent; leaves glandular-dentate, without laminar glands ..... 215. *Dutta*

211. Glycydendron Ducke, Arq. Jard. Bot. Rio Janeiro 3: 199. 1922; 4: 107, pl. 10 figs. a–

i. 1925. TYPE: *Glycydendron amazonicum* Ducke.

A monotypic genus of Amazonian Brazil. Pax & Hoffmann (1931) mistakenly reduced it to a synonym of *Nealchornea* because they misread the plate (Ducke, 1925), which contains both genera.

212. Klaineanthus Pierre ex Prain, Kew Bull. 1912: 105; Fl. Trop. Afr. 6(1): 963. 1913; Hook. Ic. Pl. 30: t. 2985. 1913; Pax & Hoffm., Pflanzenr. 147. VII (Heft 63): 408. 1914; Léonard, Fl. Congo 8(1): 130. 1962. TYPE: *Klaineanthus gaboniae* Pierre ex Prain.

A monotypic genus of West Africa (Nigeria to Gabon).

213. Tetrorchidium Poeppig in Poeppig & Endlicher, Nov. Gen. Sp. 3: 23, t. 227. 1842; Muell. Arg., DC. Prodr. 15(2): 1132. 1866; Bentham, Gen. Pl. 3: 288. 1880; Pax & Hoffm., Pflanzenr. 147. IV (Heft 52): 1912; Natürl. Pflanzenfam. ed. 2, 19c: 184. 1931; Cuatrecasas, Brittonia 9: 76. 1957; Léonard, Fl. Congo 8(1): 133. 1962; Radcliffe-Smith, Fl. E. Trop. Afr., Euphorb. 1: 373. 1987; Huft, Ann. Missouri Bot. Gard. 75: 1110. 1989. TYPE: *Tetrorchidium rubrivenium* Poepp.

Hasskarlia Baillon, Adansonia I. 1: 51. 1860 (non Meisner, 1843). *Tetrorchidiopsis* Rauschert, Taxon 31: 559. 1982. TYPE: *Hasskarlia didymostemon* Baill. [= *Tetrorchidium didymostemon* (Baillon) Pax & Hoffm.].

A genus of ca. 20 species, mostly in tropical America but ca. 5 species in Africa. The African species were referred to a separate genus *Hasskarlia* by Pax & Hoffmann (1912), but they later (Pax & Hoffmann, 1931) reduced it to a section of *Tetrorchidium*.

214. Adenocline Turczaninov, Bull. Soc. Imp. Nat. Moscou 16: 59. 1843; Muell. Arg., DC. Prodr. 15(2): 1139. 1866; Bentham, Gen. Pl. 3: 310. 1880; Prain, Ann. Bot. 27: 404. 1913; Pax & Hoffm., Pflanzenr. 147. VII (Heft 63): 409. 1914; Prain, Fl. Cap. 5(2): 488. 1920; Milne-Redhead, Kew Bull. 5: 349. 1951; Dyer, Gen. S. Afr. Fl. Pl. ed. 3, 1: 315. 1975. *Mercurialis* sect. *Adenocline* (Turcz.) Baillon, Adansonia I. 3: 159. 1864. TYPE: not designated [lectotypification not desirable at this time due to confusion in Turczaninov's application of names to specimens].

Diplostylis Sonder, Linnaea 23: 113. 1850. TYPE: *not* designated.

Paradenocline Muell. Arg., DC. Prodr. 15(2): 1141. TYPE: *Paradenocline procumbens* Muell. Arg. [= *Adenocline violifolia* (Kunze) Prain].

As treated by Prain (1920), *Adenocline* includes eight species of the Cape region of South Africa.

215. Ditta Grisebach, Mem. Amer. Acad. Arts. Sci. II. 8: 160. 1861; Muell. Arg., DC. Prodr. 15(2): 1138. 1866; Pax & Hoffm., 147. V (Heft 52): 270. 1912; Urban, Symb. Ant. 7: 261. 1912; Alain, Fl. Cuba 3: 112. 1953; Borhidi et al., Acta Agron. Acad. Sci. Hungar. 27: 432. 1978; Liogier, Fl. Española 4: 135, 348. 1986; Descr. Fl. Puerto Rico 2: 383. 1988. TYPE: *Ditta myricoides* Griseb.

A genus of one or two species of the Greater Antilles (Cuba, Hispaniola, Puerto Rico).

Subtribe 35b. ENDOSPERMINAE Pax & Hoffmann, Pflanzenr. 147. XIV (Heft 68): 53. 1919 (*nomen*); Natürl. Pflanzenfam. ed. 2, 19c: 42. 1931 (in clavi). TYPE: *Endospermum* Bentham.

Dioecious trees or shrubs, indumentum stellate; inflorescences axillary; staminate calyx gamophyllous; stamens 6–10, filaments connate; pistillode small or absent; ovary 2–6-locular; styles stigmatiform, confluent into a cap; fruit capsular.

The subtribe includes only the type genus *Endospermum*.

216. Endospermum Bentham, Fl. Hongkong. 304. 1861 (nom. cons.); Muell. Arg., DC. Prodr. 15(2): 1131. 1866; Bentham, Gen. Pl. 3: 322. 1880; Beccari, Malesia 2: 45, t. 2. 1884; Pax & Hoffmann, Pflanzenr. 147. IV (Heft 52): 33. 1912; Docters van Leeuwen, Treubia 10: 431, tt. 12, 13. 1919; Pax & Hoffm., Natürl. Pflanzenfam. ed. 2, 19c: 184. 1931; Schodde, Blumea 15: 397. 1967; Schaeffer, Blumea 19: 171. 1971; Airy Shaw, Kew Bull. Add. Ser. 8: 78. 1980. TYPE: *Endospermum chinense* Benth.

Capellenia Teijsmann & Binnendijk, Natuurk. Tijdscr. Ned.-Ind. 29: 238. 1867. TYPE: *Capellenia moluccana* Teijsm. & Binn. [= *Endospermum moluccanum* (Teijsm. & Binn.) Kurz].

A paleotropical genus of ten species, occurring

from China to Malaya, New Guinea, and tropical Australia (Queensland).

Tribe 36. GELONIEAE (Muell. Arg.) Pax, Natürl. Pflanzenfam. ed. 1, 3(5): 88. 1890. Hippomaneae subtribe Gelonieae Muell. Arg., Linnaea 34: 202. 1865; DC. Prodr. 15(2): 1124. 1866. TYPE: *Gelonium* Roxb. ex Willd. [= *Suregada* Roxb. ex Rottl.].

Dioecious (very rarely monoecious?) trees or shrubs; latex not evident; indument simple, usually very scant or absent; leaves alternate, simple, penninerved, lamina usually pellucid-punctate; stipules caducous. Inflorescences opposite the leaves; flowers apetalous, in glomerules. Staminate sepals usually 5 or 6, imbricate, free, sometimes glandular abaxially; disk extrastaminal or intrastaminal, annular or dissected; stamens (6–)10–25(–60), filaments free; anthers dehiscing longitudinally; pollen grains 2-nucleate, subglobose, 3–6-porate, exine with Croton-pattern; pistillode absent. Pistillate sepals mostly 5(4–8), imbricate, sometimes glandular abaxially; disk annular, sometimes with staminodes; ovary 3-(rarely 2- or 4-)locular; styles bifid (rarely multifid). Fruit capsular or sometimes indehiscent and drupaceous; seeds ecarunculate, seed-coat ± fleshy; endosperm present.

A monogeneric paleotropical tribe, as treated here. Pax & Hoffmann (1931), in their final treatment, construed Gelonieae as a large tribe with 18 genera in 7 subtribes; a considerable number of those genera are here included in the Adenoclineae.

217. Suregada Roxburgh ex Rottler, Ges. Naturf. Freunde Berlin, Neue Schriften 4: 206. 1803; Baillon, Etude Gén, Euphorb. 395. 1858; Croizat, Bull. Bot. Gard. Buitenzorg III. 17: 212. 1942; Merrill, J. Arnold Arbor. 37: 79. 1951; Léonard, Bull. Jard. Bot. Brux. 28: 443. 1958; Fl. Congo 8(1): 124. 1962; Radcliffe-Smith, Fl. E. Trop. Afr., Euphorb. 1: 376. 1987. TYPE: *Suregada roxburghii* Rottler.

Gelonium Roxb. ex Willd., Sp. Pl. 4: 831. 1806 (non Gaertn., 1791). TYPE: *Gelonium lanceolatum* Willd. [= *Suregada lanceolata* (Willd.) Croiz.].

Erythrocarpus Blume, Bijdr. Fl. Jav. 604. 1825. TYPE: *Erythrocarpus glomerulatus* Bl. [= *Suregada glomerulata* (Bl.) Baillon; lectotype].

Ceratophorus Sonder, Linnaea 23: 120. 1850. TYPE: *Ceratophorus africanus* Sond. [= *Suregada africana* (Sond.) Croiz.].

A paleotropical genus of ca. 40 species, the majority in tropical Asia.

Tribe 37. ELATERIOSPERMEAE Webster, Taxon 24: 599. 1975. TYPE: *Elateriospermum* Blume.

Monoecious trees; stems with whitish latex; indumentum simple; leaves alternate, pinnately veined, entire, petiole biglandular at apex; stipules caducous. Inflorescences terminal or axillary, cymose, bisexual; flowers apetalous. Staminate sepals 5, free, imbricate; disk lobed, pubescent; stamens 10–18, filaments free; anthers apiculate; pollen grains globose, inaperturate, with Croton-pattern; pistillode rudimentary or absent. Pistillate sepals 5, imbricate, caducous; disk cupular, pubescent; ovary 2–4-locular; styles unlobed, stigmas dilated. Fruit capsular but exocarp fleshy; seeds ecarunculate endosperm scanty, cotyledons massive.

A monotypic tribe including only *Elateriospermum*. The genus was placed between *Suregada* and *Endospermum* by Mueller (1866), while Bentham (1880) and Pax (1910) positioned it with *Cunuria* and *Micrandra*. The inaperturate pollen grains contradict both these positions, however. Airy Shaw (1975) included it in his subtribe Jatrophinae along with *Aleurites*, *Annesijoa*, *Tapoides*, and *Loerzingia*. The genus appears to be a relict, without any close affinities, but perhaps it is a distant relative of *Micrandra* and *Manihot*.

218. Elateriospermum Blume, Bijdr. Fl. Jav. 620. 1826; Muell. Arg., DC. Prodr. 15(2): 1130. 1866; Bentham, Hook. Ic. Pl. 13: t. 1294. 1879; Gen. Pl. 3: 288. 1880; Pax, Pflanzenr. 147. I (Heft 42): 17. 1910; J. J. Smith, Med. Dept. Landb. 10: 571. 1910; Backer & Bakh. f., Fl. Java 1: 497. 1963; Whitmore, Tree Fl. Malaya 2: 91. 1973; Airy Shaw, Kew Bull. Add. Ser. 4: 108. 1975; Kew Bull. 36: 292. 1981. TYPE: *Elateriospermum tapos* Bl. [lectotype; the other species of Blume, *E. tokbrai*, was transferred to *Blumeodendron*].

A monotypic genus of tropical southeast Asia: Thailand to Java and Borneo.

Tribe 38. JATROPHEAE (Meisner) Pax, Natürl. Pflanzen fam. ed. 1, 3(5): 72. 1890; Pflanzenr. 147. I (Heft 42): 1. 1910. Crotoneae subtribe Jatropheae Meisn., Pl. Vasc. Gen. 1: 341. 1841. Jatropheae subtribe Jatrophinae Pax, Pflanzenr. 147. I (Heft 42): 21. 1910. TYPE: *Jatropha* L.

Joannesieae (Muell. Arg.) Pax, Bot. Jahrb. 59: 142. 1924. Acalypheae subtribe Joannesieae ("Johanneseae") Muell. Arg., Linnaea 34: 201. 1865. TYPE: *Joannesia* Vell.

Monoecious (less commonly dioecious) trees, shrubs, or herbs; stems with articulated and/or nonarticulated laticifers, latex clear, white, or reddish; indumentum simple, sometimes glandular; leaves unlobed or palmately lobed or parted, usually with glands at apex of petiole; stipules persistent or deciduous. Inflorescences terminal and sometimes axillary as well, dichasial-paniculate but sometimes reduced. Staminate sepals usually 5, distinct, imbricate; petals 5, free or sometimes coherent or connate; disk entire or dissected; stamens (6)8–30, filaments at least partly connate; pollen grains globose, binucleate, inaperturate, sexine with Croton-pattern; pistillode present or absent. Pistillate sepals 5(6), free, imbricate, ± persistent in fruit; disk annular, lobed, or dissected, sometimes with staminodia; ovary mostly 2–3-locular; styles unlobed or bifid, sometimes dilated. Fruit capsular or drupaceous; seeds carunculate or ecarunculate, endosperm present.

As circumscribed here, tribe Jatropheae includes only two of the genera (*Jatropha* and *Joannesia*) assigned by Pax (1910). None of the genera enumerated for the Jatropheae by Hutchinson (1969) appear to belong in the same tribe with *Jatropha*. My previous circumscription (Webster, 1975) of the Joannesieae (a name mistakenly adopted for the Jatropheae) was broader than the present Jatropheae, since it included two genera, *Givotia* and *Ricinodendron*, that are now referred elsewhere. It might be possible to maintain two subtribes within the Jatropheae, based on *Jatropha* and *Joannesia* respectively; but *Deutzianthus* and *Oligoceras* are intermediate in many respects, and it now seems better not to recognize any subtribes within the Jatropheae.

KEY TO THE GENERA OF TRIBE JATROPHEAE

1a. Leaves simple (lobed or unlobed); monoecious or dioecious; staminate sepals free or connate; latex usually reddish.
  2a. Styles bifid or unlobed; sepals distinct; monoecious (rarely dioecious).
    3a. Fruit capsular; sepals not horned on back.
      4a. Seeds carunculate; leaves often lobed or dentate, without distinct paired glands at apex of petiole; stipules usually persistent, not infra-axillary ..... 219. *Jatropha*
      4b. Seeds ecarunculate; leaves unlobed, entire, with paired glands at apex of petiole; stipules infra-axillary, caducous ..... 220. *Vaupesia*
    3b. Fruit drupaceous; sepals horned on back ..... 221. *Oligoceras*
  2b. Styles twice bifid; staminate sepals connate below; dioecious ..... 222. *Deutzianthus*
1b. Leaves palmately compound; monoecious; seeds ecarunculate.
  5a. Styles dilated, subentire to lacinate; ovary 2-locular; anthers apiculate; foliage with malpighiaceous hairs.
    6a. Staminate calyx cupular, not covering the petals in bud; stamens 7–10, inner filaments connate; staminate disk dissected; fruit drupaceous. 223. *Joannesia*
    6b. Staminate calyx fused in bud, completely covering the petals; stamens 18–33, inner filaments connate; staminate disk annular and intrastaminal; fruit unknown ..... 224. *Leeuwenbergia*
  5b. Styles slender, bifid; ovary 3-locular; anthers muticous; foliage glabrous; staminate calyx 5-lobed; stamens 15–25, inner filaments connate; staminate disk dissected; fruit capsular ..... 225. *Annesijoa*

219. Jatropha L., Sp. Pl. 1006. 1753; Gen. Pl. ed. 5, 437. 1754; Muell. Arg., DC. Prodr. 15(2): 1076. 1866; Bentham, Gen. Pl. 3: 290. 1880; Pax, Pflanzenr. 147. I (Heft 42): 21. 1910; Hutchinson, Fl. Trop. Afr. 6(1): 775. 1912; Fawc. & Rend., Fl. Jam. 4: 310. 1920; Pax & Hoffm., Natürl. Pflanzenfam. ed. 2, 19c: 160. 1931; McVaugh, Bull. Torrey Bot. Club 72: 271. 1944; Webster, J. Arnold Arbor. 48: 340. 1967; Dehgan & Webster, Univ. California Publ. Bot. 74: 1. 1979; Radcliffe-Smith, Fl. Trop. E. Afr., Euphorb. 1: 343. 1987. *Adenoropium* Pohl, Pl. Bras. Ic. Descr. 1: 12. 1827. TYPE: *Jatropha gossypiifolia* L. [lectotype].

Curcas Adanson, Fam. Pl. 2: 356. 1763. TYPE: *Jatropha curcas* L.

Castiglionia Ruiz & Pavón, Fl. Peruv. 139. 1794. TYPE: *Castiglionia lobata* Ruiz & Pavón, nom. illeg. [= *Jatropha curcas* L.].

Loureira Cavanilles, Icon. Descr. Pl. 5: 17. 1799. TYPE: *Loureira glandulifera* Cav. [= *Jatropha cordata* (Ort.) Muell. Arg.].

Mozinna Ortega, Nov. Rar. Pl. Hort. Bot. Matr. 8: 104. 1798. TYPE: *Mozinna spathulata* Ort. [= *Jatropha dioica* Sesse].

Zimapania Engler & Pax, Natürl. Pflanzenfam. ed. 1, 3(5): 119. 1891. TYPE: *Zimapania schiedeana* Engler & Pax [= *Jatropha dioica* Sessé].

Collenucia Chiovenda, Fl. Somala 1: 177. 1929. TYPE: *Collenucia paradoxa* Chiov. [= *Jatropha paradoxa* (Chiov.) Chiov.].

A diverse genus of ca. 175 species of tropics and subtropics in the Old World and New World; native species absent from Australia and the Pacific islands. The assignment of species into subgenera and sections is given by Dehgan & Webster (1979).

220. Vaupesia Schultes, Bot. Mus. Leafl. Harvard Univ. 17: 27. 1955. TYPE: *Vaupesia cataractarum* Schultes.

A monotypic genus of the Rio Negro region, Amazonian Colombia. *Vaupesia* is a remarkable genus with latex and foliage of tribe Micrandreae but inaperturate pollen very similar to that of *Jatropha*. It may therefore represent a connecting link between tribes Micrandreae and Jatropheae; Schultes (pers. comm.) regards it as better placed in the Micrandreae.

221. Oligoceras Gagnepain, Bull. Soc. Bot. France 71: 872. 1925; Fl. Indochine 5: 467. 1926; Airy Shaw, Kew Bull. 14: 392. 1960. TYPE: *Oligoceras eberhardtii* Gagnep.

A monotypic genus of Indochina; closely related to *Deutzianthus* but distinguished by its monoecious flower production and curious horned sepals.

222. Deutzianthus Gagnepain, Bull. Soc. Bot. France 71: 139. 1924; Fl. Indochine 5: 297. 1925; Wu, Acta Phytotax. Sin. 6: 245. 1957; Airy Shaw, Kew Bull. 14: 362. 1960; 16: 346. 1963. TYPE: *Deutzianthus tonkinensis* Gagnep.

Loerzingia Airy Shaw, Kew Bull. 16: 365. 1963; 25: 543. 1972; 36: 312. 1980, syn. nov. TYPE: *Loerzingia thyrsiflora* Airy Shaw [= **Deutzianthus thyrsiflorus** (Airy Shaw) Webster, comb. nov.].

A genus of two species, in Indochina and Sumatra. Airy Shaw compared his *Loerzingia* with *Tapoides* Airy Shaw from Borneo; however, the staminate calyx, with distinct imbricate lobes, suggests a closer affinity to tribe Jatropheae. Comparison of the illustrations of Gagnepain (1926) and Airy Shaw (1981) indicates that in fact the Sumatran *Loerzingia* is extremely similar to the Indochinese *Deutzianthus*, and their differences seem of specific rather than generic value.

223. Joannesia Vellozo, Alogr. Alkalis 199. 1798; Muell. Arg., DC. Prodr. 15(2): 715. 1866; Bentham, Gen. Pl. 3: 290. 1880; Pax, Pflanzenr. 147. I (Heft 42): 116. 1910; Ducke, Arch. Jard. Bot. Rio de Janeiro 3: 198. 1922; Schultes, Bot. Mus. Leafl. Harvard Univ. 17: 25. 1955; Smith et al., Fl. Ilustr. Catar., EUFO 165. 1988. TYPE: *Joannesia princeps* Vell.

Anda A. Juss., Tent. Euphorb. 3. 1824. TYPE: *Anda gomesii* A. Juss., nom. illeg. [= *Joannesia princeps* Vell.].

Andicus Vellozo, Fl. Flum. 80, t. 86. 1825. TYPE: *Andicus pentaphyllus* Vell. [= *Joannesia princeps* Vell.].

A neotropical genus of two South American species.

224. Leeuwenbergia Letouzey & Hallé, Adansonia II. 14: 379. 1974. TYPE: *Leeuwenbergia letestui* Letouzey & Hallé.

A tropical west African genus of two species in Cameroon, Congo, and Gabon. The genus is in many ways intermediate between *Joannesia* and *Annesijoa*, but the type species (*L. letestui*) differs strikingly from both in having a completely gamophyllous calyx that splits open on anthesis as in genera of Aleuritideae. Unfortunately, the staminate flowers of the second species, *Leeuwenbergia africana* Let. & Hallé, are still unknown.

225. Annesijoa Pax & Hoffmann, Pflanzenr. 147. XIV (Heft 68): 9. 1919; Airy Shaw, Kew Bull. 16: 345. 1963; Hook. Ic. Pl. 38: t. 3713. 1974; Kew Bull. Add. Ser. 8: 27. 1980. TYPE: *Annesijoa novoguineensis* Pax & Hoffm.

A monotypic genus endemic to New Guinea.

Tribe 39. CODIAEAE (Pax) Hutchinson, Amer. J. Bot. 56: 747. 1969. Clutieae subtribe Codiaeinae Pax, Pflanzenr. 147. III (Heft 47): 10. 1911. TYPE: *Codiaeum* Rumph. ex A. Juss.

Monoecious or dioecious trees or shrubs; stems with nonarticulated laticifers, latex clear (sometimes reddish) and nontoxic; indumentum simple or stellate; leaves penninerved or triplinerved, unlobed, usually eglandular; stipules often caducous, sometimes obsolete. Inflorescences terminal or axillary, racemose or paniculate. Staminate sepals 4–6, free or connate, imbricate or valvate; petals mostly 5, free, usually imbricate; disk dissected or lobed; stamens (5–)10–100 or more, free or basally connate; pollen grains binucleate, globose, inaperturate, sexine with Croton-pattern; pistillode absent. Pistillate sepals 4, usually imbricate, sometimes accrescent; petals usually 5, sometimes absent; disk annular (rarely dissected or absent); ovary mostly 3-locular; styles unlobed to bipartite. Fruit capsular; columella usually persistent; seeds carunculate or ecarunculate, testa sometimes fleshy; endosperm present.

This tribe of 15 genera with over 100 species has the greatest generic diversity in the Crotonoideae, and relationships between the genera are not clear; it seems premature to attempt to recognize formal subtribes at this time.

KEY TO THE GENERA OF TRIBE CODIAEAE

1a. Petals present, at least in staminate flowers.
  2a. Petals present in pistillate flowers.
    3a. Staminate calyx lobed; fruit capsular.
      4a. Leaves without beadlike glands beneath; anthers and petals not gland-tipped; inflorescences terminal or axillary, not opposite the leaves.
        5a. Inflorescences terminal; seeds carunculate; staminate disk and receptacle glabrous.
          6a. Ovary 3-locular; petals glabrous outside ..... 226. *Baloghia*
          6b. Ovary 2-locular; petals golden-sericeous outside ..... 227. *Hylandia*
        5b. Inflorescences axillary; staminate disk or receptacle pilose.
          7a. Indumentum simple; styles bifid ..... 228. *Ostodes*
          7b. Indumentum (in inflorescence) malpighiaceous; staminate disk cupular.
            8a. Styles bifid; staminate disk glabrous; stamens mostly 5–7; petals pubescent adaxially; seeds carunculate ..... 229. *Pausandra*
            8b. Styles multifid; staminate disk pubescent; stamens 14 16; petals not pubescent adaxially; seeds ecarunculate ..... 230. *Dodecastigma*
      4b. Leaves with beadlike glands beneath; anthers and petals with apical glands; inflorescences opposite the leaves ..... 231. *Pantadenia*
    3b. Staminate calyx almost truncate.
      9a. Pistillate calyx accrescent; petals glabrous; fruit capsular ..... 232. *Dimorphocalyx*
      9b. Pistillate calyx not accrescent; petals tomentose; fruit drupaceous ..... 233. *Fontainea*
  2b. Petals absent in pistillate flowers.
    10a. Inflorescences axillary.
      11a. Flowers in racemes; stipules caducous or absent; anthers muticous.
        12a. Styles entire, slender ..... 234. *Codiaeum*
        12b. Styles twice bifid ..... 235. *Sphyranthera*
      11b. Flowers in axillary clusters; stipules persistent, ± spinose; anthers apiculate; styles bifid or dilated ..... 236. *Acidocroton*
    10b. Inflorescences terminal.
      13a. Pistillate sepals accrescent, not recurved; floral disk present.
        14a. Pistillate sepals eglandular; seeds mostly ecarunculate ..... 237. *Blachia*
        14b. Pistillate sepals glandular; seeds carunculate ..... 238. *Strophioblachia*
      13b. Pistillate sepals recurved, not accrescent; floral disk absent ..... 239. *Sagotia*
1b. Petals absent; styles bifid; seeds carunculate; leaves glandular ..... 240. *Baliospermum*

226. Baloghia Endlicher, Prodr. Fl. Norf. 84. 1833; Bentham, Gen. Pl. 3: 300. 1880; Pax, Pflanzenr. 147. III (Heft 47): 12. 1911; Maiden, For. Fl. N. S. W. 1: 165, t. 28. 1904; White, Proc. Roy. Soc. Queensl. 53: 226. 1942; Airy Shaw, Kew Bull. 35: 598. 1980; McPherson & Tirel, Fl. Nouv.-Caléd. 14(1): 43. 1987; James & Harden, Fl. N. S. W. 1: 410, 1990. TYPE: *Baloghia lucida* Endl.

Steigeria Muell. Arg., Linnaea 34: 215. 1865; DC. Prodr. 15(2): 1121. 1866. TYPE: *Steigeria montana* Muell. Arg. [= *Baloghia montana* (Muell. Arg.) Pax].

An Australasian genus of 15 species, 12 in New Caledonia and the others in Norfolk Island, Lord Howe Island, and Australia.

227. Hylandia Airy Shaw, Kew Bull. 29: 329. 1974; 35: 643, fig. 4. 1980. TYPE: *Hylandia dockrillii* Airy Shaw.

A monotypic genus of tropical Australia (Queensland). Airy Shaw (1974) suggested a relationship with *Dimorphocalyx*, *Ostodes*, and *Loerzingia* (*Deutzianthus*), especially the latter. These suggestions are generally compatible with the present treatment, but it appears that *Baloghia* may prove to be the closest genus.

228. Ostodes Blume, Bijdr. Fl. Ned. Ind. 619. 1825; Muell. Arg. 15(2): 1114. 1866; Bentham, Gen. Pl. 3: 299. 1880; Hook. f., Fl. Brit. Ind. 5: 400. 1887; Pax & Hoffm., Pflanzenr. 147. III (Heft 47): 17. 1911; Gagnepain, Fl. Indochine 5: 322. 1925; Airy Shaw, Kew Bull. 20: 409. 1966; 26: 311. 1971; 35: 334. 1981. TYPE: *Ostodes paniculata* Bl.

As circumscribed by Airy Shaw (1966), *Ostodes* is a genus of four species of tropical Asia, from the eastern Himalayas to northern Borneo. A number of species included by Pax & Hoffmann (1911) were removed by Airy Shaw (1966) to *Fahrenheitia*, a disposition that is accepted here pending further study.

229. Pausandra Radlkofer, Flora 53: 92, t. 2. 1870; Baillon, Adansonia I. 11: 92. 1873; Muell. Arg., Fl. Brasil. 11(2): 503, t. 99.

1874; Pax & Hoffm., Pflanzenr. 147. III (Heft 47): 41. 1911; Lanjouw, Rec. Trav. Bot. Neerl. 33: 758. 1936; Jablonski, Mem. New York Bot. Gard. 17: 153. 1967; Secco, Bol. Mus. Par. Emilio Goeldi, Bot. 3: 59. 1987; Huft, Ann. Missouri Bot. Gard. 75: 1115. 1989; Secco, Rev. Gen. *Anomalocalyx* . . . Amer. Sul 58. 1990. TYPE: *Pausandra morisoniana* (Casar.) Radlk.

As revised by Secco (1990), *Pausandra* is a neotropical genus of ca. eight species, extending from Honduras to Brazil. The genus is very distinctive and isolated from other genera of the tribe except for *Dodecastigma*, which is similar in indumentum and staminate disk, but very different in a number of other characters.

230. Dodecastigma Ducke, Notizbl. Bot. Gart. Berlin 11: 343. 1932; Arq. Jard. Bot. Rio Janeiro 6: 58, t. 5. 1933; Sandwith, Kew Bull. 1950: 134. 1951; Jablonski, Mem. New York Bot. Gard. 17: 154. 1967; Secco, Rev. Gen. *Anomalocalyx* . . . Amer. Sul 42. 1990. TYPE: *Dodecastigma amazonicum* Ducke.

A genus of two species of the Brazilian Amazon and the Guianas.

231. Pantadenia Gagnepain, Bull. Soc. Bot. France 71: 873. 1925; Fl. Indochine 5: 470. 1926; Airy Shaw, Kew Bull. 28: 122. 1969; 26: 312. 1972. TYPE: *Pantadenia adenanthera* Gagn.

Parapantadenia Capuron, Adansonia II. 12: 206. 1972. TYPE: *Parapantadenia chauvetiae* Leandri [= **Pantadenia chauvetiae** (Leandri) Webster, comb. nov.].

A paleotropical genus of two widely disjunct species, one endemic to Madagascar, the other found in Thailand and Indochina. The genus *Parapantadenia* was distinguished by the 2-locular ovary that develops into a 1-seeded, indehiscent fruit. However, the species are otherwise so similar in the peculiar indumentum and inflorescence that it seems best to regard them as congeneric.

232. Dimorphocalyx Thwaites, Enum. Pl. Zeyl. 278. 1861; Bentham, Gen. Pl. 3: 301. 1880; Hook. f., Fl. Brit. Ind. 5: 403. 1887; Trimen, Handb. Fl. Ceylon 4: 54, pl. 84. 1898; Pax, Pflanzenr. 147. III (Heft 47): 31. 1911; Airy Shaw, Kew Bull. 23: 123. 1969; 26: 251. 1972; Whitmore, Tree Fl. Malaya 2: 86. 1973; Airy Shaw, Kew Bull. Add. Ser. 4: 95. 1975; Kew Bull. 35: 624. 1980. TYPE: *Dimorphocalyx glabellus* Thw.

A genus of ca. 15 species, mainly in tropical Asia (India and Sri Lanka to Hainan and Borneo) but extending to Australia.

233. Fontainea Heckel, Etudes sur *Fontainea pancheri*. 1870; Baillon, Hist. Pl. 5: 194. 1874; Pax, Pflanzenr. 147. III (Heft 47): 30. 1911; Airy Shaw, Kew Bull. 35: 632. 1980; Jessup & Guymer, Austrobaileya 2: 112. 1985; McPherson & Tirel, Fl. Nouv.-Caléd. 14(1): 74. 1987. TYPE: *Fontainea pancheri* (Baillon) Heckel.

An Australasian genus of six species, extending from Australia to New Guinea, New Caledonia, and Vanuatu.

234. Codiaeum Rumphius ex A. Jussieu, Euphorb. Tent. 33. 1824 (nom. cons.); Muell. Arg., DC. Prodr. 15(2): 1116. 1866; Bentham, Gen. Pl. 3: 299. 1880; Pax, Pflanzenr. 147. III (Heft 47): 23. 1911; Airy Shaw, Kew Bull. Add. Ser. 4: 88. 1975; 8: 62. 1980; A. C. Smith, Fl. Vitiensis Nova 2: 549. 1981; McPherson & Tirel, Fl. Nouv.-Caléd. 14(1): 95. 1987. TYPE: *Codiaeum variegatum* (L.) A. Juss.

Phyllaurea Loureiro, Fl. Cochinch. 575. 1790. TYPE: *Phyllaurea codiaeum* Lour. [nom. illeg., = *Codiaeum variegatum* (L.) A. Juss.].

Synapisma Endlicher, Gen. Pl. 1110. 1840. TYPE: *Crozophora peltata* Labill. [= *Codiaeum peltatum* (Labill.) P. Green].

Junghuhnia Miquel, Fl. Ind. Batav. 1(2): 412. 1859 (non Corda, 1842). TYPE: *Junghuhnia glabra* Miq. [= *Codiaeum variegatum* (L.) A. Juss.].

An Australasian genus of ca. 15 species, from Borneo and the Philippines to New Guinea, tropical Australia, New Caledonia, and the Pacific islands. Mueller (1866) adopted an extremely broad concept of *Codiaeum*, including *Baloghia* and *Blachia* as sections; however, recent workers concur in the narrower definition.

235. Sphyranthera Hooker f., Hook. Ic. Pl. 18: t. 1702. 1887; Chakrabarty & Vasudeva Rao, J. Econ. Tax. Bot. 5: 959. 1984; 6: 429. 1985. TYPE: *Sphyranthera capitellata* Hook. f., nom. illeg. [= *Sphyranthera lutescens* (Kurz) Pax & Hoffm.].

An endemic genus of the Andaman/Nicobar archipelago; there are two species, the type and the recently described *S. airyshawii* Chakrab. &

Vasud. The relationships of the genus are still uncertain; Hooker suggested that *Sphyranthera* might belong to the Acalypheae.

236. Acidocroton Grisebach, Fl. Br. W. Ind. 42. 1859 (nom. cons. prop.; proposed here); Muell. Arg., DC. Prodr. 15(2): 1042. 1866; Bentham, Gen. Pl. 3: 291. 1880; Pax, Pflanzenr. 147. I (Heft 42): 13. 1910; Urban, Symb. Ant. 7: 513. 1913; Fawc. & Rend., Fl. Jam. 4: 316. 1920; Urban, Symb. Ant. 9: 208. 1924; Ark. Bot. 20A(15): 62. 1926; Alain, Fl. Cuba 3: 73. 1953; Fl. Española 4: 69. 1986. TYPE: *Acidocroton adelioides* Griseb.

Ophellantha Standley, J. Wash. Acad. Sci. 14: 97. 1924; syn. nov. TYPE: *Ophellantha spinosa* Standl., op. cit. 98 [= **Acidocroton spinosus** (Standl.) Webster, comb. nov.].

A mainly Caribbean genus of 12 species, 2 from Central America (Chiapas/Guatemala) and the remainder from the Greater Antilles, with the majority in Cuba (an undescribed species is reported from Colombia by Huft; pers. comm.). The genus has been subject to both nomenclatural and taxonomic problems since its description. Grisebach cited *Acidoton* P. Brown and *Adelia acidoton* L. as the basis for his genus and type species; unfortunately, the Jamaican plant of Browne and Linnaeus represents *Flueggea acidoton* (L.) Webster (Allertonia 3: 299. 1984). Although Grisebach's description is indeed based on material of the genus accepted by later authors as *Acidocroton*, by typification his genus is a synonym of *Flueggea*. Conservation of this genus that is common and widespread in the Greater Antilles would seem to be the best solution.

Although *Ophellantha*, described from Central America, has been accepted as a distinct genus (e.g., by Standley & Steyermark, Fieldiana Bot. 24(6): 139. 1949), it has never been compared with *Acidocroton*. While the two taxa appear different in aspect because of the reduced leaves and greater spinosity of the West Indian plants, they are very similar in floral characters except for the more accrescent calyx in the Central American plants. It therefore appears that *Ophellantha* is best treated as **Acidocroton** sect. **Ophellantha** (Standl.) Webster, comb. nov. The only other species in the section besides the type is **Acidocroton steyermarkii** (Standl.) Webster, comb. nov. [*Ophellantha steyermarkii* Standley, Field Mus. Bot. 23: 123. 1944].

The affinities of *Acidocroton* have been variously interpreted. Mueller (1866) created for it a subtribe placed between *Pogonophora* and *Clutia*. Bentham (1880) suggested an affinity with *Jatropha*; and Pax (1910), apparently following Bentham's lead, referred *Acidocroton* to tribe Jatropheae, but located it in subtribe Micrandrinae adjacent to *Garcia*. Although the matter still needs more study, the totality of floral characters support a placement in tribe Codiaeae.

237. Blachia Baillon, Etude Gén. Euphorb. 385. 1858; Bentham, Gen. Pl. 3: 301. 1880; Hook. f., Fl. Brit. Ind. 5: 402. 1887; Pax, Pflanzenr. 147. III (Heft 47): 36. 1911; Gagnepain, Fl. Indochine 5: 410. 1926; Airy Shaw, Kew Bull. 23: 121. 1969; 26: 223. 1972; Kew Bull. Add. Ser. 4: 57. 1975; Thin, Tap Chi Sinh Hoc 11(3): 16. 1989. TYPE: *Blachia umbellata* (Willd.) Baill. [*Croton umbellatus* Willd.].

A genus of ca. ten species, in tropical Asia from southern India to Hainan, the Philippines, and perhaps Borneo. The genus appears related to *Acidocroton* of the New World, especially the section *Ophellantha*.

238. Strophioblachia Boerlage, Handl. Fl. Ned. Ind. 3(1): 235. 1900; Pax, Pflanzenr. 147. III (Heft 47): 35. 1911; Merrill, Univ. California Publ. Bot. 10: 425. 1925; Gagnepain, Fl. Indochine 5: 408. 1926; Airy Shaw, Kew Bull. 25: 544. 1971; Thin, Tap Chi Sinh Hoc 11(3): 15. 1989. TYPE: *Strophioblachia fimbricalyx* Boerl.

A genus of two species in southeast Asia: Indochina to Hainan, the Philippines, and Celebes.

239. Sagotia Baillon, Adansonia I. 1: 53. 1860 (nom. cons.); Muell. Arg., DC. Prodr. 15(2): 1113. 1866; Fl. Bras. 11(2): 504. 1874; Bentham, Gen. Pl. 3: 302. 1880; Pax, Pflanzenr. 147. III (Heft 47): 39. 1911; Jablonski, Mem. New York Bot. Gard. 17: 151. 1967; Secco, Acta Amazonica 15(1 2, suppl.): 81. 1985; Rev. Gen. *Anomalocalyx* . . . Amer. Sul 99. 1990. TYPE: *Sagotia racemosa* Baillon.

According to Secco (1985), *Sagotia* includes two species of Amazonian South America; Levin (pers. comm.) also reports the genus from Costa Rica and Panama. The systematic position of the genus is rather doubtful; it shows some resemblances to *Ostodes* but also to *Croton* and related genera.

240. Baliospermum Blume, Bijdr. Fl. Ned. Ind. 603. 1826; Decaisne in Jacquemont, Voy. Inde Atlas 2: t. 155. 1844; Muell. Arg., DC. Prodr. 15(2): 1125. 1866; Hook. f., Fl. Brit. Ind. 5: 461. 1887; J. J. Smith, Meded. Dept. Landb. 10: 599. 1910; Pax & Hoffm., Pflanzenr. 147. IV (Heft 52): 24. 1912; Gagnepain, Fl. Indochine 5: 429. 1926; Airy Shaw, Kew Bull. 26: 222. 1972; 36: 267. 1981; Thin, Tap Chi Sinh Hoc 11(3): 16. 1989. TYPE: *Baliospermum axillare* Bl.

An Asian genus of ca. 12 species, distributed from India to China (Yunnan) and Java. Mueller (1866) associated *Baliospermum* with *Gelonium*, which it somewhat resembles in habit, and has been followed in this by Pax & Hoffmann (1912) and other later workers. However, the nonaperturate pollen is quite different from that of *Suregada*, and Airy Shaw (1975) seems closer to the mark in referring it to his "subtribe Codiaeinae" along with *Codiaeum*, *Blachia*, and *Strophioblachia*. Thin (1989) has described a new section, *Dioicea*, based on *Baliospermum balansae* Gagnep.

Tribe 40. TRIGONOSTEMONEAE Webster, Taxon 24: 599. 1975. TYPE: *Trigonostemon* Bl.

Monoecious trees or shrubs; indumentum simple; leaves alternate, unlobed, pinnately veined, sometimes stipellate at base but lacking paired glands at apex of petiole; stipules persistent or deciduous, often small. Inflorescences terminal or axillary, racemose or thyrsoid. Staminate sepals 5, free, imbricate; petals 5, exceeding the calyx; disk cupular or dissected; stamens 3(–5), filaments connate, anther connective enlarged, often elongated; pollen grains globose, inaperturate, with Croton-pattern, sexinous processes small; pistillode absent. Pistillate sepals 5, free, imbricate; disk cupular; ovary 3-locular; styles free or nearly so, unlobed or bifid. Fruit capsular; seeds ecarunculate, testa dry; endosperm present.

The tribe contains the single paleotropical genus *Trigonostemon*.

241. Trigonostemon Blume, Bijdr. Fl. Ned. Ind. 600. 1825 (as *Trigostemon*); Fl. Javae Praef. viii. 1828 (nom. cons.); Muell. Arg., DC. Prodr. 15(2): 1105. 1866; Bentham, Gen. Pl. 3: 298. 1880; Hook. f., Fl. Brit. Ind. 5: 395. 1887; Pax & Hoffm., Pflanzenr. 147. III (Heft 47): 85. 1911; Gagnepain, Fl. Indochine 5: 309. 1925; Quisumbing, Phil. J. Sci. 41: 329. 1930; Jablonski, Brittonia 15: 151. 1963; Airy Shaw, Kew Bull. 23: 126. 1969; 25: 545. 1971; Whitmore, Tree Fl. Malaya 2: 134. 1973; Airy Shaw, Kew Bull. Add. Ser. 4: 201. 1975; Kew Bull. 35: 352. 1981. TYPE: *Trigonostemon serratus* Bl.

Enchidium Jack, Malayan Misc. 2(7): 89. 1822 (nom. rej.). TYPE: *Enchidium verticillatum* Jack [= *Trigonostemon verticillatus* (Jack) Pax].

Silvaea Hook. & Arn., Bot. Beechey's Voy. 211. 1837. TYPE: *Silvaea semperflorens* (Roxb.) Hook. & Arn. [= *Trigonostemon semperflorens* (Roxb.) Muell. Arg.].

Athroisma Griffith, Not. Pl. As. 4: 477. 1854 (non A. P. DeCandolle, 1833. TYPE: not designated (Griffith cited two species, neither positively identified by Pax & Hoffmann [1911]).

Telogyne Baillon, Etude Gén. Euphorb. 327. 1858. TYPE: *Telogyne indica* Baill. [= *Trigonostemon verticillatus* (Jack) Pax].

Tritaxis Baillon, Etude Gén. Euphorb. 342. 1858. TYPE: *Tritaxis gaudichaudii* Baillon [= *Trigonostemon gaudichaudii* (Baill.) Muell. Arg.].

Tylosepalum Kurz ex Teysm. & Binn., Natuurk. Tijdschr. Ned.-Indië 27: 50. 1864. TYPE: *Tylosepalum aurantiacum* Kurz ex Teysm. & Binn. [= *Trigonostemon aurantiacus* (Kurz ex Teysm. & Binn.) Boerl.].

Nepenthandra Sp. Moore, J. Bot. 43: 149. 1905. TYPE: *Nepenthandra lanceolata* Sp. Moore [= *Trigonostemon lanceolatus* (Sp. Moore) Pax].

Prosartema Gagnepain, Bull. Soc. Bot. France 71: 875. 1925. TYPE: *Prosartema stellaris* Gagnep. [= *Trigonostemon stellaris* (Gagnep.) Airy Shaw].

Poilaniella Gagnepain, Bull. Soc. Bot. France 72: 467. 1925. TYPE: *Poilaniella fragilis* Gagnep. [= *Trigonostemon fragilis* (Gagnep.) Airy Shaw].

Neotrigonostemon Pax & Hoffm., Notizbl. Bot. Gart. Berlin 10: 385. 1928. TYPE: *Neotrigonostemon diversifolius* Pax & Hoffm. [= *Trigonostemon viridissimus* (Kurz) Airy Shaw].

Kurziodendron Balakrishnan, Bull. Bot. Surv. India 8: 68. 1966. TYPE: *Kurziodendron viridissimum* (Kurz) Balakr. [= *Trigonostemon viridissimus* (Kurz) Airy Shaw].

A rather diverse genus of tropical Asia, extending from India and Sri Lanka to New Guinea. The diversity of the genus is clearly indicated by the remarkably extensive generic synonymy. The relationships of the genus have been differently understood. Mueller (1866), who accepted a broad circumscription (including *Dimorphocalyx*), referred *Trigonostemon* to the Jatropheae. Pax & Hoffmann (1911) included it in tribe Clutieae subtribe Clutiinae, where it is clearly out of place. Airy Shaw (1975) placed it in his informal "subtribe" Ostodinae along with *Fahrenheitia* and *Dimorphocalyx*. This placement has much to recommend it, and it is possible that the tribe Trigonostemoneae cannot be maintained as distinct from the Codiaeae.

Tribe 41. RICINOCARPEAE Muell. Arg., Bot. Zeit. 22: 324. 1864; DC. Prodr. 15(2): 199. 1866. Subfam. Ricinocarpoideae Pax, Natürl. Pflanzenfam. ed. 1, 3(5): 113. 1890. Family Ricinocarpaceae (Muell. Arg.) Hurusawa, J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 6: 224. 1954. TYPE: *Ricinocarpos* Desf.

Monoecious (rarely dioecious) shrubs or herbs; latex scanty or apparently absent; indumentum stellate, glandular hairs often present; leaves alternate, entire, often ericoid, eglandular, exstipulate. Inflorescences terminal or axillary, racemose or reduced to clusters or solitary flowers. Staminate sepals 4–6, free, imbricate, often petaloid; petals usually 5, or absent; disk dissected or absent; stamens mostly 15 or more, filaments connate into a column or short and apparently free; anthers extrorse; pollen grains globose, inaperturate, sexine with modified Croton-pattern (processes spinose, or reduced); pistillode absent. Pistillate sepals (4)5, imbricate; petals 5, sometimes reduced or absent; disk dissected or absent; ovary 3-locular; styles unlobed, bifid, or multifid. Fruit capsular, 1–3-locular; seeds carunculate; endosperm present; embryo cylindrical, with narrow cotyledons.

As indicated by pollen characters, tribe Ricinocarpeae definitely belongs in subfamily Crotonoideae and not in a separate group of "Stenolobeae" as treated by Mueller (1866), Bentham (1880), and Pax & Hoffmann (1931). The tribe appears rather closely related to the Crotoneae, and further work may show that the two groups should be combined.

KEY TO THE SUBTRIBES OF TRIBE RICINOCARPEAE

1a. Pollen grains with large clavate sexinous processes; petals and disk usually present; ovary 3-locular; leaves alternate ..... 41a. Ricinocarpinae
1b. Pollen grains with reduced sexinous processes; petals and disk absent; ovary 1 3-locular; leaves alternate, opposite, or whorled ..... 41b. Bertyinae

Subtribe 41a. RICINOCARPINAE Webster, Taxon 24: 599. 1975. TYPE: *Ricinocarpos* Desf.

Trees, shrubs, or undershrubs; leaves alternate, sometimes resinous; flowers in terminal or axillary racemes or clusters (or solitary); sepals distinct or connate; petals usually present, longer or shorter than sepals; stamens 20 or more, filaments free (or inner connate at base); pollen grains with large clavate processes; ovary 3-locular; styles bifid or unlobed; fruit capsular, with 3 seeds.

An Australasian group of three genera, two endemic to Australia.

KEY TO THE GENERA OF SUBTRIBE RICINOCARPINAE

1a. Styles bifid to multifid; stamens at least partially connate.
2a. Staminate calyx lobed halfway or more; filaments all connate; petioles short ..... 242. *Ricinocarpos*
2b. Staminate calyx lobed less than halfway; outer filaments free; petioles long ..... 243. *Alphandia*
1b. Styles unlobed, dilated, forming a cap over the ovary; stamens all free ..... 244. *Beyeria*

242. Ricinocarpos Desfontaines, Mém. Mus. Hist. Nat. Paris 3: 459, t. 22. 1817; Muell. Arg., DC. Prodr. 15(2): 203. 1866 (as *Ricinocarpus*); Bentham & Mueller, Fl. Austral. 6: 68. 1873; Bentham, Gen. Pl. 3: 263. 1880; Maiden, Ill. N. S. W. Pl., t. 16. 1908; Grüning, Pflanzenr. 147 (Heft 58): 37. 1913; Pax & Hoffm., Natürl. Pflanzenfam. ed. 2, 19c: 226. 1931; Stanley, Fl. S.-E. Queensland 1: 432. 1983. TYPE: *Ricinocarpos pinifolius* Desf.

Roeperia Sprengel, Syst. Veg. 3: 147. 1826. TYPE: *Roeperia pinifolia* (Desf.) Spreng. [= *Ricinocarpos pinifolius* Spreng.].

An Australian genus of ca. 15 species grouped into 4 sections by Grüning. Although reported from New Caledonia, it does not occur there; the supposed New Caledonian species has been transferred to *Baloghia* by McPherson & Tirel (1987).

243. Alphandia Baillon, Adansonia I. 11: 85. 1873; Pax & Hoffmann, Pflanzenr. 147. III (Heft 47): 22. 1911; Airy Shaw, Kew Bull. Add. Ser. 8: 27. 1980; McPherson & Tirel, Fl. Nouv.-Caléd. 14(1): 86. 1987. TYPE: *Alphandia furfuracea* Baillon.

A Melanesian genus of three species in New Guinea, New Caledonia, and Vanuatu.

244. Beyeria Miquel, Ann. Sci. Nat. III. 1: 350, t. 15. 1844; Muell. Arg., DC. Prodr. 15(2): 201. 1866; Bentham & Mueller, Fl. Austral. 6: 63. 1873; Bentham, Gen. Pl. 3: 263. 1880; Grüning, Pflanzenr. 147. (Heft 58): 63. 1913; Pax & Hoffm., Natürl. Pflanzenfam. ed. 2, 19c: 227. 1931; James & Harden, Fl. N. S. W. 1: 412. 1990. TYPE: *Beyeria viscosa* (Labill.) Miq.

Calyptrostigma Klotzsch in Lehm., Pl. Preiss. 1: 175. 1845. TYPE: *Calyptrostigma viscosum* (Labill.) Kl. [= *Beyeria viscosa* (Labill.) Miq.].

Beyeriopsis Muell. Arg., Linnaea 34: 56. 1865. TYPE: *Beyeriopsis brevifolia* Muell. Arg. [= *Beyeria brevifolia* (Muell. Arg.) Benth.; lectotype, designated by Wheeler, 1975].

A genus of ca. 15 species endemic to Australia.

Subtribe 41b. BERTYINAE Muell. Arg., Linnaea 34: 56. 1865; DC. Prodr. 15(2): 208. 1866. TYPE: *Bertya* Planchon.

Trees or shrubs; leaves alternate, opposite, or verticillate; flowers in axillary racemes or clusters (or solitary); sepals distinct or absent; petals present or absent; stamens numerous, filaments connate into a column, anthers often pubescent; pollen grains with sexinous processes reduced; ovary 2–3 locular; styles bifid to multifid; fruit 1–3-seeded.

This Australasian subtribe includes one genus from Australia, two from New Caledonia, and one from Borneo.

KEY TO THE GENERA OF SUBTRIBE BERTYINAE

1a. Staminate sepals present; petals present or absent; ovary 3-locular.
  2a. Leaves alternate; anthers glabrous; fruit usually 1-seeded ..... 245. *Bertya*
  2b. Leaves opposite or whorled; anthers pubescent; fruit 3-seeded.
    3a. Leaves opposite; inflorescences racemose, terminal; styles multifid ..... 246. *Myricanthe*
    3b. Leaves whorled; inflorescences 1-flowered, axillary; styles 2–4-fid ..... 247. *Cocconerion*
1b. Staminate sepals absent; petals absent; ovary 2-locular; staminate flowers in terminal bracteate catkins, pistillate solitary, axillary; anthers pubescent; styles bifid ..... 248. *Borneodendron*

245. Bertya Planchon, Hook. Lond. J. Bot. 4: 472. 1845; Muell. Arg., DC. Prodr. 15(2): 208. 1866; Bentham & Mueller, Fl. Austral. 6: 74. 1873; Bentham, Gen. Pl. 3: 264. 1880; Grüning, Pflanzenr. 147. (Heft 58): 49. 1913; Pax & Hoffm., Natürl. Pflanzenfam. ed. 2, 19c: 226. 1931; Guymer, Austrobaileya 2: 427. 1988; James & Harden, Fl. N. S. W. 1: 414. 1990. TYPE: *Bertya rosmarinifolia* Planchon [lectotype, chosen here].

A genus of ca. 20 species endemic to Australia.

246. Myricanthe Airy Shaw, Kew Bull. 35: 390. 1980; McPherson & Tirel, Fl. Nouv.-Caléd. 14(1): 72. 1987. TYPE: *Myricanthe discolor* Airy Shaw.

A monotypic genus restricted to northwestern New Caledonia.

247. Cocconerion Baillon, Adansonia 11: 87. 1873; Guillaumin, Fl. Syn. Nouv.-Caléd. 189. 1948; Airy Shaw, Kew Bull. 25: 503. 1971; 32: 382. 1978; McPherson & Tirel, Fl. Nouv.-Caléd. 14(1): 38. 1987. TYPE: *Cocconerion balansae* Baillon.

A genus of two species endemic to New Caledonia.

248. Borneodendron Airy Shaw, Kew Bull. 16: 359. 1963; Hook. Ic. Pl. 7(2): t. 3633. 1967; Kew Bull. Add. Ser. 4: 60. 1975. TYPE: *Borneodendron aenigmaticum* Airy Shaw.

A monotypic genus endemic to Borneo. In the original description, Airy Shaw (1963) compared *Borneodendron* to *Baloghia*, a genus that it somewhat resembles in foliar characters. Later (Airy Shaw, 1975), he regarded it as most closely allied with *Cocconerion*, a disposition that is followed here.

Tribe 42. CROTONEAE Dumort., Anal. Fam. Pl. 45. 1829 ("Crotonieae"). TYPE: *Croton* L.

Monoecious or dioecious trees, shrubs, or herbs; stems with nonarticulated laticifers; latex clear or reddish, often scanty or apparently absent; indumentum stellate or lepidote; leaves alternate, simple to palmately lobed, sometimes pellucid-punctate; petiole with or without apical paired glands; stipules present or absent. Inflorescences terminal or axillary, racemose or spicate. Staminate sepals mostly 5, imbricate to valvate, free; petals 5, imbricate, sometimes absent; disk annular or dissected, receptacle often villose; stamens 3–400, filaments free, often inflexed in bud; anthers muticous; pollen grains globose, inaperturate, with sexinous Croton-pattern; pistillode absent. Pistillate sepals 4–7(–10), ± free, sometimes accrescent, imbricate to reduplicate-valvate; petals 5, mostly reduced or obsolete; ovary mostly 3-locular; styles free or nearly so, once to several times bifid. Fruit capsular; seeds carunculate, testa dry; endosperm copious.

The circumscription of tribe Crotoneae is expanded from my previous treatment (Webster, 1975), in which only *Croton* and the two satellite genera *Crotonopsis* and *Eremocarpus* were included. The suggested inclusion of *Mildbraedia*, *Fahrenheitia*, and *Moacroton* in the tribe is still rather shakily supported and requires further evaluation, but at least has the merit of not leaving

Croton in a taxonomic "black box" without any apparent relatives.

KEY TO THE GENERA OF TRIBE CROTONEAE

1a. Filaments not distinctly inflexed in bud; pistillate flowers petaliferous.
  2a. Stamens 10–30; staminate petals thinner in texture than sepals; pistillate flowers petaliferous; styles bifid.
    3a. Stamens free; staminate petals free; inflorescences axillary; seed coat dry ..... 249. *Mildbraedia*
    3b. Stamens with filaments connate; staminate petals coherent; inflorescences terminal; seed coat fleshy ..... 250. *Fahrenheitia*
  2b. Stamens 3–6; staminate petals similar in texture to sepals; pistillate flowers apetalous; styles unlobed or emarginate ..... 251. *Moacroton*
1b. Filaments ± distinctly inflexed in bud; pistillate petals mostly reduced to absent ..... 252. *Croton*

249. Mildbraedia Pax, Bot. Jahrb. 43: 319. 1909; Pflanzenr. 147. III (Heft 47): 11. 1911; Hutchinson, Fl. Trop. Afr. 6(1): 798. 1912; Léonard, Fl. Congo Belge 8(1): 85. 1962; Radcliffe-Smith, Fl. E. Trop. Afr., Euphorb. 1: 340. 1987. TYPE: *Mildbraedia paniculata* Pax.

Neojatropha Pax, Pflanzenr. 147. I (Heft 42): 114. 1910. TYPE: *Neojatropha carpinifolia* (Pax) Pax [= *Mildbraedia carpinifolia* (Pax) Hutch.].

A tropical African genus of four species.

250. Fahrenheitia Reichb. f. & Zoll., Linnaea 28: 599. 1856; Muell. Arg., DC. Prodr. 15(2): 1256. 1866; Airy Shaw, Kew Bull. 20: 409. 1966; 26: 270. 1972; Whitmore, Tree Fl. Malaya 2: 97. 1973; Airy Shaw, Kew Bull. Add. Ser. 4: 114. 1975; Kew Bull. 36: 298. 1981. TYPE: *Fahrenheitia collina* Reichb. f. & Zoll. [= *Fahrenheitia pendula* (Hassk.) Airy Shaw].

A tropical Asian genus of four species, found from southern India and Sri Lanka to the Philippines and Borneo. Pax & Hoffmann (1911) included the then-known species within *Ostodes*, but Airy Shaw (1966) showed that *Fahrenheitia* was quite distinct, although he later (Airy Shaw, 1975) referred it to the same informal "subtribe" as *Ostodes*.

251. Moacroton Croizat, J. Arnold Arbor. 26: 189. 1945; Alain, Fl. Cuba 3: 85. 1953. TYPE: *Moacroton leonis* Croiz.

As defined by Croizat and Alain, *Moacroton* is a genus of six species endemic to Cuba. It appears closely related to *Croton*, and its status requires evaluation (Webster, 1992).

252. Croton L., Sp. Pl. 2: 1004. 1753; Gen. Pl., ed. 5, 436. 1754; Klotzsch, Hook. London J. Bot. 2: 48. 1843; Muell. Arg., DC. Prodr. 15(2): 512. 1866; Fl. Bras. 11(1): 81. 1873; Bentham, Gen. Pl. 3: 293. 1880; Hook. f., Fl. Brit. Ind. 5: 385. 1887; Ferguson, Rep. Missouri Bot. Gard. 12: 33. 1901; Hutchinson, Fl. Trop. Afr. 6(1): 746. 1912; Gagnepain, Fl. Indochine 5: 256. 1925; Pax & Hoffm., Natürl. Pflanzenfam. ed. 2, 19c: 83. 1931; Leandri, Ann. Inst. Bot.-Geol. Colon. Marseille, V. 7(1): 1. 1939; Carabia, Carib. For. 3: 114. 1942; Croizat, Darwiniana 5: 417. 1941; 6: 442. 1944; Johnston & Warnock, Southw. Nat. 7: 1. 1962; Webster, J. Arnold Arbor. 48: 353. 1967; Leandri, Adansonia II. 10: 191. 1970; Liogier, Fl. Española 4: 108. 1986; Thin, Tap Chi Sinh Hoc 8(2): 28. 1986; Webster, Ann. Missouri Bot. Gard. 75: 1116. 1989; Novon 2: 270. 1992; Taxon 42: 793. 1993. TYPE: *Croton aromaticus* L. [lectotype, designated by Webster, J. Arnold Arbor. 48: 354. 1967; this replaced the earlier but incorrect selection of *Croton tiglium* L. by Small, in Britton & Brown, Ill. Fl. N. U.S. ed. 2, 2: 254. 1913].

Cieca Adanson, Fam. Pl. 2: 355. 1763 (nom. rej.). TYPE: *Croton argenteus* L.

Crotonopsis Michaux, Fl. Bor.-Amer. 2: 185. 1803. *Leptemon* Raf., Med. Repos. II. 5: 353. 1808 (nom. superfl.). TYPE: *Crotonopsis linearis* Michaux [= *Croton michauxii* Webster].

Friesia Sprengel, Anleit. Kenntn. Gewächse, ed. 2, 2(2): 885. 1818. TYPE: *Friesia argentea* Sprengel [= *Croton michauxii* Webster].

Decarinium Raf., Neogenyton 1. 1825. TYPE: *Decarinium glandulosum* (L.) Raf. [= *Croton glandulosus* L.].

Drepadenium Raf., Neogenyton 2. 1825. TYPE: *Drepadenium maritimum* (Walt.) Raf. [= *Croton maritimus* Walt.].

Heptallon Raf., Neogenyton 1. 1825. TYPE: *Heptallon graveolens* Raf. [= *Croton capitatus* Michx.; lectotype, chosen here].

Julocroton Martius, Flora 20(2) Beibl.: 119. 1837. TYPE: *Julocroton phagedaenicus* Mart. [= *Croton triqueter* Lam.].

Astrogyne Bentham, Pl. Hartweg. 14. 1839. TYPE: *Astrogyne crotonoides* Benth. [= *Croton diocus* Cav.].

Astraea Klotzsch, Arch. Naturgesch. 7: 194. 1841. TYPE: *Astraea lobata* (L.) Kl. [= *Croton lobatus* L.].

Cleodora Klotzsch, Arch. Naturgesch. 7: 196. 1841. TYPE: *Cleodora sellowiana* Kl. [= *Croton sphaerogynus* Baill.].

Eutropia Klotzsch, Arch. Naturgesch. 7: 196. 1841.

TYPE: *Eutropia brasiliensis* Kl., nom. illeg. [= *Croton polyandrus* Spreng.].

Medea Klotzsch, Arch. Naturgesch. 7: 193. 1841. TYPE: *Medea hirta* Klotzsch [= *Croton timandroides* (Didr.) Muell. Arg.].

Ocalia Klotzsch, Arch. Naturgesch. 7: 195. 1841. TYPE: *Croton perdicipes* St. Hil. [= *Croton antisiphiliticus* Mart., lectotype, designated by Wheeler, 1975].

Pilinophytum Klotzsch, Arch. Naturgesch. 7: 255. 1841. TYPE: *Pilinophytum capitatum* (Michx.) Kl. [= *Croton capitatus* Michx.].

Podostachys Klotzsch, Arch. Naturgesch. 7: 193. 1841. TYPE: *Podostachys subfloccosa* Didr. [= *Croton lundianus* (Didr.) Muell. Arg. var. *subfloccosa* (Didr.) Muell. Arg.; lectotype, designated by Wheeler (1975)].

Timandra Klotzsch, Arch. Naturgesch. 7: 197. 1841. TYPE: *Croton serratus* Muell. Arg. [lectotype, designated by Wheeler (1975)].

Heterochlamys Turcz., Bull. Soc. Imp. Nat. Moscou 16: 61. 1843. TYPE: *Heterochlamys quinquinervia* Turcz. [= *Croton argenteus* L.].

Lasiogyne Klotzsch, Nov. Act. Acad. Caes. Leop.-Carol. Nat. Cur. 19(suppl.)1: 418. 1843. TYPE: *Lasiogyne brasiliensis* Kl. [= *Croton compressus* Lam.].

Tiglium Klotzsch, Nov. Act. Acad. Caes. Leop.-Carol. Nat. Cur. 19(suppl.)1: 418. 1843. TYPE: *Tiglium officinale* Kl. (nom. illeg.) [= *Croton tiglium* L.].

Eremocarpus Bentham, Bot. Voy. Sulphur 53. 1844. *Piscaria* Piper, Contr. U.S. Nat. Herb. 11: 382. 1906 (nom. superfl.). TYPE: *Eremocarpus setigerus* (Hook.) Benth. [= *Croton setigerus* Hook.].

Angelandra Endlicher, Gen. Pl. Suppl. 5: 91. 1850. TYPE: *Croton ellipticus* Nutt., non *C. ellipticus* Geiseler [= *Croton lindheimerianus* Scheele].

Barhamia Klotzsch, in Seem., Bot. Voy. Herald 104. 1853. TYPE: *Barhamia panamensis* Kl. [= *Croton hircinus* Vent.; lectotype, designated by Wheeler (1975)].

Cyclostigma Klotzsch, in Seem., Bot. Voy. Herald 104. 1853. TYPE: *Cyclostigma panamensis* Kl. [= *Croton draco* Schlecht. ssp. *panamensis* (Kl.) Webster; designated by Wheeler (1975)].

Gynamblosis Torrey, Rep. Marcy Exped. 295. 1853. TYPE: *Gynamblosis monanthogyna* (Michx.) Torr. [= *Croton monanthogynus* Michx.].

Centrandra Karsten, Linnaea 28: 440. 1857. TYPE: *Centrandra hondensis* Karst. [= *Croton hondensis* (Karst.) Webster].

Myriogomphos Didrichsen, Vidensk. Medd. Dansk Naturh. Foren. Kjoebenhavn 1857: 142. 1857. TYPE: *Myriogomphos fuscus* Didr. [= *Croton fuscus* (Didr.) Muell. Arg.].

Heterocroton Spencer Moore, Trans. Linn. Soc. II. 4: 461. 1895. TYPE: *Heterocroton mentiens* Sp. Moore [= *Croton mentiens* (Sp. Moore) Pax].

A large and highly diverse but definitely monophyletic genus of at least 800 species, the majority American but also with more than 200 paleotropical species. Only a selection of the more important references has been given here. The complexity of the genus is indicated by the 40 sections recently discriminated (Webster, 1993).

The relationships of *Croton* within the family have been obscured by the fact that it has generally been referred to a separate tribe associated only with the satellite genera *Crotonopsis*, *Eremocarpus*, and *Julocroton*. However, these commonly accepted segregate genera cannot be maintained under a phylogenetic circumscription of *Croton* (Webster, 1992). The African genus *Mildbraedia* seems to be a likely candidate for the sister group, since it has in common characters of indumentum, flowers, and seeds, but it diverges in its axillary, unisexual, more or less cymose inflorescences. The 3-nucleate pollen grains of *Croton* suggest a possible relationship with the tribe Ricinocarpeae.

Tribe 43. RICINODENDREAE (Pax) Hutchinson, Amer. J. Bot. 56: 749. 1969. Cluytieae subtribe Ricinodendrinae Pax, Natürl. Pflanzenfam. ed. 1, 3(5): 87. 1890. TYPE: *Ricinodendron* Muell. Arg.

Dioecious trees or shrubs; indumentum stellate; leaves alternate, unlobed to lobed or palmatisect; stipules entire to lobed, or absent. Inflorescences axillary or the pistillate terminal, paniculate or reduced to clusters or solitary flowers. Staminate sepals 4 or 5, imbricate; petals 5, ± coherent into a tube; disk dissected or lobed; stamens (3)5–20, filaments united below; pistillode absent. Pistillate sepals 4 or 5, imbricate; petals 5, coherent; disk lobed; ovary 1–3-locular; styles bifid. Fruit drupaceous, 1–3-seeded; seeds ecarunculate; endosperm copious, oily.

This paleotropical tribe of two genera is entirely African or Madagascan except for one species in India. Relationships of the tribe are uncertain. *Givotia* suggests *Jatropha* in its habit, but diverges in its stellate indumentum and different inflorescence; nevertheless, Ricinodendreae may be related to Jatropheae.

KEY TO THE GENERA OF TRIBE RICINODENDREAE

1a. Leaves unlobed to 5-lobed; stipules small, unlobed ..... 253. *Givotia*

1b. Leaves palmately parted.

2a. Stipules flabellate-lobed, persistent; ovary mostly 2–3-locular; endocarp smooth, thin-walled ..... 254. *Ricinodendron*

2b. Stipules small, unlobed, deciduous; ovary mostly 1-locular; endocarp pitted, thick-walled ..... 255. *Schinziophyton*

253. Givotia Griffith, Calcutta J. Nat. Hist. 4: 88. 1843; Muell. Arg., DC. Prodr. 15(2): 1112. 1866; Bentham, Gen. Pl. 3: 297. 1880;

Pax & Hoffm., Pflanzenr. 147. III (Heft 47): 44. 1911; Radcliffe-Smith, Kew Bull. 22: 493. 1968; Fl. Trop. E. Afr. Euphorb. 1: 329. 1987. TYPE: *Givotia rottleriformis* Griffith ex Wight.

A genus of four species, one from Africa, two from Madagascar, and one from India.

254. Ricinodendron Muell. Arg., Flora 47: 533. 1864; DC. Prodr. 15(2): 1111. 1866; Bentham, Hook. Ic. Pl. 13: t. 1300. 1879; Gen. Pl. 3: 297. 1880; Pax, Pflanzenr. 147. III (Heft 47): 45. 1911; Mildbraed, Notizbl. Bot. Gart. Berlin 12: 516. 1935; Léonard, Fl. Congo 8(1): 116. 1962; Radcliffe-Smith, Fl. E. Trop. Afr. Euphorb. 1: 325. 1987. TYPE: *Ricinodendron africanus* Muell. Arg.

A genus of two African species, closely related to *Givotia* and apparently differing only in vegetative characters.

255. Schinziophyton Hutchinson ex Radcliffe-Smith, Kew Bull. 45: 157. 1990. TYPE: *Schinziophyton rautanenii* (Schinz) Radcl.-Sm.

A monotypic African genus, discriminated by Hutchinson in an unpublished manuscript and characterized by Radcliffe-Smith as distinct from *Ricinodendron* in a number of characters, including its truly compound leaves, small stipules, and large fruits with deeply pitted endocarp.

Tribe 44. ALEURITIDEAE Hurusawa, J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 6: 309. 1954. TYPE: *Aleurites* G. Forster.

Monoecious trees or shrubs; stems with nonarticulated laticifers, latex scanty or absent; indumentum simple or stellate; leaves alternate, pinnately to palmately veined or lobed, eglandular or with laminar glands; stipules present or absent. Inflorescences terminal or axillary, dichasial-paniculate or reduced to cymose clusters. Staminate calyx closed in bud, splitting into valvate segments; petals mostly 5(6–13), free, imbricate; disk dissected or of intrastaminal segments; stamens 8–20(–100), filaments free; pollen grains globose, inaperturate, with Croton-pattern; pistillode absent. Pistillate sepals and petals as in staminate; disk lobed, dissected, or obsolete; ovary 2–5-locular; styles bifid. Fruit drupaceous or capsular and tardily dehiscent; seeds ecarunculate, testa dry; endosperm copious, oily.

Tribe Aleuritideae is circumscribed as previously (Webster, 1975) to include 5 subtribes with a total of 15 genera and 45–50 species. It is overwhelmingly paleotropical, with only two American genera. The tribe as presently constituted is still not satisfactorily defined. Bentham (1880) included *Aleurites* and other genera of Aleuritideae within the Jatropheae. There are indeed many points of similarity between *Aleurites* and *Jatropha*, and Bentham's disposition is much better than that of Pax & Hoffmann (1931), who included *Aleurites* in a very artificial subtribe along with *Agrostistachys*. *Joannesia* has characters that suggest both the Jatropheae and Aleuritideae, and it may prove desirable to resurrect tribe Joannesieae (Pax, 1924) in order to arrive at a more natural classification.

KEY TO THE SUBTRIBES OF TRIBE ALEURITIDEAE

1a. Monoecious.
  2a. Petals 5, glabrous; stamens 8–20, filaments connate; inflorescence paniculate; leaves palmately veined or lobed ..... 44a. Aleuritinae
  2b. Petals 6–13, sericeous; stamens 30–100, filaments free; inflorescence a cymose cluster; leaves pinnately veined ..... 44b. Garciinae

1b. Dioecious.
  3a. Petals present, at least in staminate flower.
    4a. Indumentum simple or absent; petals free; inflorescence mostly terminal ..... 44c. Grosserinae
    4b. Indumentum stellate or lepidote; petals often coherent or connate; inflorescence terminal or axillary ..... 44d. Crotonogyninae
  3b. Petals absent; indumentum stellate; leaves with beadlike glands ..... 44e. Neoboutoninae

Subtribe 44a. ALEURITINAE (Hurusawa) Webster, Taxon 24: 599. 1975. TYPE: *Aleurites* J. R. & G. Forster.

Monoecious trees or shrubs; indumentum simple or stellate; leaf blades palmately veined or lobed, with glands at apex of petiole; inflorescence ± paniculate; staminate calyx segments 2 or 3; petals 5, free, glabrous; disk-segments 5; stamens 8–20, inner filaments connate; ovary 2- or 3-locular; fruit drupaceous or capsular; seeds ecarunculate.

The subtribe Aleuritinae is here equivalent to the tribe Aleuritideae of Hurusawa (1954), except that the genus *Aleurites* is treated as subdivided into three genera, following Airy Shaw (1967). There is considerable doubt whether these segregates need to be recognized, as I indicated earlier

(Webster, 1967); however, they are provisionally accepted here, pending further critical study.

KEY TO THE GENERA OF SUBTRIBE ALEURITINAE

1a. Ovary 2-locular; fruit drupaceous; stamens 15–20, anthers introrse; indumentum distinctly stellate ..... 256. *Aleurites*
1b. Ovary 3–5-locular; fruit dehiscent; stamens 7–12.
2a. Indumentum stellate; anthers extrorse; inflorescence densely pubescent, bracts conspicuous ..... 257. *Reutealis*
2b. Indumentum of bifid or simple hairs; anthers introrse; inflorescence not densely pubescent, bracts inconspicuous ..... 258. *Vernicia*

256. Aleurites J. R. & G. Forster, Charact. Gen. Pl. 111, t. 56. 1776; Muell. Arg., DC. Prodr. 15(2): 722. 1866; Bentham, Gen. Pl. 3: 292. 1880; Hemsley, Hook. Ic. Pl. 29: t. 2801, 2802. 1909; Pax, Pflanzenr. 147. I (Heft 42): 128. 1910; Gagnepain, Fl. Indochine 5: 290. 1925; Airy Shaw, Kew Bull. 20: 393. 1967; Webster, J. Arnold Arbor. 48: 342. 1967; Walker, Fl. Okinawa 644. 1976; Smith, Fl. Vitiensis Nova 2: 547. 1981; Radcliffe-Smith, Fl. E. Trop. Afr., Euphorb. 1: 176. 1987. TYPE: *Aleurites triloba* J. R. & G. Forster [= *Aleurites moluccana* (L.) Willd.].

In the restricted sense adopted by Airy Shaw (1967), *Aleurites* is a genus of two species extending from India to the Pacific islands.

257. Reutealis Airy Shaw, Kew Bull. 20: 394. 1967. TYPE: *Reutealis trisperma* (Blanco) Airy Shaw.

A monotypic genus endemic to the Philippines; more or less intermediate between *Aleurites* (sensu stricto) and *Vernicia*.

258. Vernicia Loureiro, Fl. Cochinch. 586. 1790; Hemsley, Hook. Ic. Pl. 29: t. 2801, 2802. 1906 (under *Aleurites*); Airy Shaw, Kew Bull. 20: 394. 1967; Radcliffe-Smith, Fl. E. Trop. Afr., Euphorb. 1: 178. 1987. TYPE: *Vernicia montana* Lour.

An Asian genus of three species distributed from Burma to Indochina, China, and Japan; found in more temperate latitudes or elevations than *Aleurites* and *Reutealis*.

Subtribe 44b. GARCIINAE Muell. Arg., Linnaea 34: 143. 1865; DC. Prodr. 15(2): 719. 1866; Pax & Hoffm., Pflanzenr. 147. XIV (Heft 68): 9. 1919. TYPE: *Garcia* Vahl in Rohr.

Monoecious trees or shrubs; indumentum simple; leaves entire, pinnately veined, without glands at apex of petiole, exstipulate; inflorescences terminal, reduced to cymose clusters; petals 6–13, sericeous; staminate disk dissected, intrastaminal; stamens 30–100, filaments free; ovary 3-locular; styles bifid; fruit capsular; seeds ecarunculate.

Although Mueller (1866) included three other genera (*Aleurites*, *Crotonogyne*, and *Manniophyton*) in his subtribe Garciinae, Pax & Hoffmann (1919) removed them. In the treatment of Webster (1975), this monogeneric delimitation was followed, and it is still accepted here.

259. Garcia Vahl in Rohr, Skriv. Naturh.-Selsk. Kjobenh. 2: 217, t. 9. 1792; Muell. Arg., DC. Prodr. 15(2): 721; Lundell, Wrightia 1: 1. 1945; Webster, Ann. Missouri Bot. Gard. 54: 238. 1968. TYPE: *Garcia nutans* Vahl ex Rohr.

A neotropical genus of two species distributed from Mexico to Colombia.

Subtribe 44c. GROSSERINAE Webster, Taxon 24: 600. 1975. TYPE: *Grossera* Pax.

Dioecious trees or shrubs; indumentum simple or absent; leaves pinnately veined or triplinerved, glandular or eglandular; stipules deciduous or absent; inflorescences terminal, racemose or paniculate; staminate petals 4 or 5, free; stamens 6–40, filaments free or connate; pistillate petals 4 or 5, free; ovary 3–5-locular; styles bifid; fruit capsular; seeds ecarunculate.

The seven genera of this subtribe are American/African in distribution, except for *Tapoides* from Indonesia.

KEY TO THE GENERA OF SUBTRIBE GROSSERINAE

1a. Sexinous processes of pollen rounded to obtuse; leaves pinnately veined.
2a. Staminate petals glabrous; leaves pellucid-punctate.
3a. Bracts large, imbricate, caducous, forming a cone before anthesis; leaves entire; stipular scars subannular, conspicuous; pistillate sepals unthickened ..... 260. *Cavacoa*
3b. Bracts small, persistent, not forming a cone before anthesis; leaves denticulate; stipule scars very small; pistillate sepals medially thickened ..... 261. *Grossera*

2b. Staminate petals pubescent; leaves not pellucid-punctate.
4a. Inflorescences axillary; seeds ecarunculate; staminate disk annular.
5a. Stamens 6–8; capsule tomentose ..... 262. *Tapoides*
5b. Stamens over 20; capsule glabrous ..... 263. *Anomalocalyx*
4b. Inflorescences terminal; seeds carunculate; staminate disk dissected; stamens over 20; capsule tomentose ..... 264. *Sandwithia*
1b. Sexinous processes of pollen echinate; leaves triplinerved; staminate disk dissected.
6a. Pistillate sepals 4 or 5, imbricate; staminate receptacle glabrous ..... 265. *Tannodia*
6b. Pistillate sepals 2 or 3; staminate receptacle pilose ..... 266. *Domohinea*

260. Cavacoa Léonard, Bull. Jard. Bot. Brux. 25: 320. 1955; Fl. Congo Belge 8(1): 191. 1962; Elffers & Taylor, Hook. Ic. Pl. 36: t. 3561. 1956; Radcliffe-Smith, Fl. E. Trop. Afr., Euphorb. 1: 174. 1987. *Grossera* sect. *Racemiformes* Pax & Hoffm., Pflanzenr. 147. VI (Heft 57): 105. 1912. TYPE: *Cavacoa quintasii* (Pax & Hoffm.) Léonard [*Grossera quintasii* Pax & Hoffm.].

A genus of three species of central and east Africa.

261. Grossera Pax, Bot. Jahrb. 33: 281. 1903; Pax & Hoffm., Pflanzenr. 147. VI (Heft 57): 105. 1912; Cavaco, Bull. Mus. Hist. Nat. Paris 21: 272. 1949; Léonard, Bull. Jard. Bot. Brux. 25: 316. 1955; Bull. Jard. Bot. Brux. 28: 118. 1958; Fl. Congo 8(1): 188. 1962. TYPE: *Grossera paniculata* Pax [lectotype, designated by Léonard, 1955].

An African genus of seven species.

262. Tapoides Airy Shaw, Kew Bull. 14: 473. 1960; 20: 412. 1966; Hook. Ic. Pl. 37: t. 3632. 1967; Kew Bull. Add. Ser. 4: 200. 1975. TYPE: *Tapoides villamilii* (Merr.) Airy Shaw [*Ostodes villamilii* Merr.].

A monotypic genus of Borneo.

263. Anomalocalyx Ducke, Notizbl. Bot. Gart. Berlin 11: 344. 1932; Arq. Jard. Bot. Rio Janeiro 6: 60. 1933; Secco, Rev. Gen. *Anomalocalyx* . . . Amer. Sul 39. 1990. TYPE: *Anomalocalyx uleanus* (Pax) Ducke.

A monotypic genus of Amazonian Brazil. The phylogenetic position of *Anomalocalyx* is dubious, and it possibly belongs close to *Dodecastigma* and *Sagotia*.

264. Sandwithia Lanjouw, Kew Bull. 1932: 184. 1933; Secco, Bull. Mus. Par. Emilio Goeldi Bot. 3: 157. 1987; 4: 177. 1988. TYPE: *Sandwithia guyanensis* Lanj.

A genus of two species of the Guyana region and Amazonian Brazil and Venezuela. Secco (1988) regarded *Sagotia* as the most closely related genus, an opinion that needs careful consideration. *Sandwithia* is here provisionally retained in subtribe Grosserinae because of its resemblance to *Anomalocalyx*, but it is quite possible that all three genera may prove to belong to the same tribe or subtribe.

265. Tannodia Baillon, Adansonia I. 1: 251. 1861; Muell. Arg., DC. Prodr. 15(2): 728. 1866; Bentham, Gen. Pl. 3: 304. 1880; Pax & Hoffm., Pflanzenr. 147. VI (Heft 57): 110. 1912; Prain, J. Bot. 50: 125. 1912; Léonard, Bull. Jard. Bot. Brux. 25: 300. 1955; Fl. Congo 8(1): 186. 1962; Radcliffe-Smith, Fl. E. Trop. Afr., Euphorb. 1: 172. 1987. *Tandonia* Baillon, Adansonia I. 1: 184. 1861 (non *Tandonia* Moq.-Tand., 1849). TYPE: *Tannodia cordifolia* (Baill.) Baill. [*Tandonia cordifolia* Baill.].

Holstia Pax, Bot. Jahrb. 43: 220. 1909. *Tannodia* sect. Holstia (Pax) Prain, J. Bot. 50: 127. 1912. *Neoholstia* Rauschert, Taxon 31: 559. 1982 (nom. superfl.). TYPE: *Holstia tenuifolia* Pax [= *Tannodia tenuifolia* (Pax) Prain; lectotype].

A genus of three or four species in east Africa and the Comoro Islands. Although Radcliffe-Smith (1987a) maintained *Holstia* (as *Neoholstia*) as a distinct genus, it differs only in a relatively trivial perianth character, and Prain's reduction of it to a section of *Tannodia* appears justified.

266. Domohinea Leandri, Bull. Soc. Bot. France 87: 285. 1940. TYPE: *Domohinea perrieri* Leandri.

A monotypic genus from Madagascar. In describing it, Leandri noted its affinity to *Grossera* and *Tannodia*, and this disposition appears correct.

Subtribe 44d. CROTONOGYNINAE Webster, Taxon 24: 600. 1975. TYPE: *Crotonogyne* Muell. Arg.

Trees or shrubs, sometimes scandent; indumentum stellate or lepidote; leaves pinnately or pal-

mately veined, biglandular at juncture with petiole, stipulate; inflorescences axillary, spicate or racemose to paniculate; staminate petals coherent or connate; staminate disk dissected; stamens 7–40, filaments free or connate; anthers often apiculate; pistillate sepals 4 or 5, imbricate or valvate; disk cupular; ovary 3-locular; styles bifid or multifid; fruit capsular; seeds ecarunculate.

An African tribe of three genera. *Crotonogyne* and *Manniophyton* were originally referred to subtribe Garciinae by Mueller (1866); however, they differ from *Garcia* in having stellate indumentum, dioecious inflorescences, and fewer petals that are more or less coherent. The Crotonogyninae seem most closely related to the Grosserinae.

KEY TO THE GENERA OF SUBTRIBE CROTONOGYNINAE

1a. Trees or shrubs; leaves pinnately veined; petioles lacking inflated trichomes.
  2a. Styles bifid; inflorescences terminal, paniculate; staminate petals free; staminate disk receptacular and extrastaminal, of more than 10 segments ..... 267. *Cyrtogonone*
  2b. Styles multifid; inflorescences axillary, racemose or spicate; staminate petals mostly coherent or connate; staminate disk extrastaminal, of 5–8 segments ..... 268. *Crotonogyne*
1b. Lianas; leaves palmately veined; petioles with inflated trichomes; styles bifid; staminate petals connate ..... 269. *Manniophyton*

267. Cyrtogonone Prain, Kew Bull. 1911: 231. 1911; Pax & Hoffm., Pflanzenr. 147. VI (Heft 57): 111. 1912; Prain, Hook. Ic. Pl. 31: t. 3008. 1915; Keay, Fl. W. Trop. Afr., ed. 2, 1: 399. 1958. TYPE: *Cyrtogonone argentea* (Pax) Prain [*Crotonogyne argentea* Pax].

A monotypic genus of west Africa (Nigeria to Cameroon).

268. Crotonogyne Muell. Arg., Flora 47: 535. 1864; DC. Prodr. 15(2): 720. 1866; Bentham, Gen. Pl. 3: 305. 1880; Pax & Hoffm., Pflanzenr. 147. VI (Heft 57): 111. 1912; Prain, Hook. Ic. Pl. 31: t. 3019. 1915; Léonard, Fl. Congo 8(1): 174. 1962; Adam, Fl. Mt. Nimba 468, t. 165. 1971. TYPE: *Crotonogyne manniana* Muell. Arg.

Neomanniophyton Pax & Hoffm., Pflanzenr. 147. VI (Heft 57): 115. 1912. TYPE: *Neomanniophyton impeditum* (Prain) Pax [= *Crotonogyne impedita* Prain; lectotype, chosen here].

A genus of 15 species in west Africa (Sierra Leone to Congo and Angola).

269. Manniophyton Muell. Arg., Flora 47: 530. 1864; DC. Prodr. 15(2): 719. 1866; Bentham, Hook. Ic. Pl. 13: t. 1267. 1878; Gen. Pl. 3: 297. 1880; Pax & Hoffm., Pflanzenr. 147. VI (Heft 57): 120. 1912; Keay, Fl. W. Trop. Afr., ed. 2, 1: 400. 1954; Léonard, Bull. Jard. Bot. Brux. 25: 290. 1955; Fl. Congo 8(1): 171. 1962; Adam, Mém. Mus. Hist. Nat. Paris 20: 495, t. 183. 1971. TYPE: *Manniophyton africanum* Muell. Arg.

A monotypic genus of west Africa (Sierra Leone to Angola and Príncipe).

Subtribe 44e. NEOBOUTONINAE (Hutchinson) Webster, Taxon 24: 600. 1975. Acalypheae subtribe Mercurialinae ser. Neoboutoniiformes Pax & Hoffm., Pflanzenr. 147. VII (Heft 63): 71. 1914. Tribe Neoboutonieae Hutch., Amer. J. Bot. 56: 752. 1969. TYPE: *Neoboutonia* Muell. Arg.

Tribe Benoistieae Radcliffe-Smith, Kew Bull. 43: 632. 1988. TYPE: *Benoistia* Perrier & Leandri.

Dioecious trees or shrubs; indumentum stellate or lepidote; leaves unlobed, pinnately or palmately veined, glandular-dotted, stipulate; inflorescences terminal or axillary, racemose to paniculate; calyx-segments 2 or 3; disk dissected or absent; stamens 15–40, filaments free, shorter than anthers; anthers with glandular connective; ovary 3-locular; styles bifid; fruit capsular; seeds carunculate or ecarunculate.

A subtribe of two genera, one African and one Madagascan. The two genera are quite distinct, and Radcliffe-Smith (1988) has proposed to place *Benoistia* in a separate tribe. However, *Neoboutonia* and *Benoistia* still seem more closely related to one another than to other taxa, so they are provisionally kept in the same subtribe.

KEY TO THE GENERA OF SUBTRIBE NEOBOUTONINAE

1a. Leaves palmately veined; stipules persistent; seeds carunculate ..... 270. *Neoboutonia*
1b. Leaves pinnately veined; stipules deciduous; seeds ecarunculate ..... 271. *Benoistia*

270. Neoboutonia Muell. Arg., J. Bot. 2: 336. 1864; DC. Prodr. 15(2): 892. 1866; Bentham, Hook. Ic. Pl. 13: t. 1298, 1299. 1879; Gen. Pl. 3: 317. 1880; Pax & Hoffm., Pflanzenr. 147. VII (Heft 63): 71. 1914; Robyns, Fl. Sperm. Parc Nat. Albert 1: 451, t. 44. 1948; Radcliffe-Smith, Fl. E. Trop. Afr., Eu-

phorb. 1: 231. 1987. TYPE: *Neoboutonia africana* Muell. Arg.

A genus of three African species.

271. Benoistia Perrier & Leandri, Bull. Soc. Bot. France 85: 528. 1938; Radcliffe-Smith, Kew Bull. 43: 632. 1988. TYPE: *Benoistia perrieri* Leandri [lectotype, chosen here].

A Madagascan genus of three species.

Subfamily V. EUPHORBIOIDEAE. TYPE: *Euphorbia* L.

Subfamily Sapioideae Hurusawa, J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 6: 310. 1954. TYPE: *Sapium* P. Browne.

Monoecious or less commonly dioecious trees, shrubs, or herbs (rarely scandent); laticifers nonarticulated, latex usually whitish, sometimes scanty or apparently absent; indumentum simple or absent (dendritic in *Mabea*); leaves alternate or opposite, simple and unlobed, entire or dentate, usually pinnately veined, often with glands at base of blade; stipules usually small, often reduced or absent. Inflorescences terminal or axillary, spicate to racemose, paniculate, or pseudanthial (cyathium); bracts often biglandular at base; flowers apetalous. Staminate sepals 3–6, imbricate to valvate, mostly open in bud, commonly reduced or obsolete; disk absent; stamens 1–20(–70), filaments free or connate; pollen grains oblate to prolate, 3-colporate, colpi usually marginate, sexine usually tectate-perforate; pistillode absent. Pistillate sepals 3–6, free or connate, imbricate or open in bud, sometimes reduced or obsolete; disk absent; ovary 2–3(–20)-locular; styles nearly always unlobed, free or commonly connate into a column. Fruit capsular (rarely drupaceous); seeds carunculate or ecarunculate, testa dry or fleshy; endosperm copious.

The circumscription of subfamily Euphorbioideae and its five tribes is essentially the same as that adopted earlier (Webster, 1975). It corresponds roughly to the tribes Hippomaneae and Euphorbieae in the sense of Pax & Hoffmann (1931), except that the tribe Stomatocalyceae (included in the Gelonieae by Pax & Hoffmann) is added.

KEY TO THE TRIBES OF SUBFAMILY EUPHORBIOIDEAE

1a. Pollen sexine reticulate; inflorescences racemose or paniculate, bracts eglandular; stamens 10–30, free; staminate calyx 3–8-lobed; styles undivided; seeds ecarunculate; dioecious trees or lianas ——— 45. STOMATOCALYCEAE

1b. Pollen sexine perforate-tectate; inflorescences mostly racemose, spicate, or pseudanthial; bracts mostly glandular or adnate to rachis; stamens 1–many, free or connate; monoecious (rarely dioecious) trees, shrubs or herbs, not scandent.
2a. Inflorescences mostly racemose or spicate (if capitate, then not pseudanthial); styles mostly undivided; staminate calyx usually developed.
3a. Floral bracts usually biglandular at base, not peltate nor adnate to the rachis; stamens free or connate.
4a. Staminate calyx open in bud; leaves mostly not spinulose-dentate; stamens free or filaments connate; seeds carunculate or ecarunculate ... 46. HIPPOMANEAE
4b. Staminate calyx closed in bud, valvately dehiscent into 2 segments; leaves spinose-dentate; filaments and anthers connate; seeds ecarunculate ——— 47. PACHYSTROMATEAE
3b. Floral bracts eglandular, peltate or adnate to the rachis and covering flowers; seeds ecarunculate ... 48. HUREAE
2b. Inflorescences pseudanthial (cyathial), usually with a single terminal pistillate flower and 4 or 5 lateral staminate monochasia or dichasia; perianth reduced or absent; styles mostly bifid; seeds carunculate or ecarunculate ——— 49. EUPHORBIEAE

Tribe 45. STOMATOCALYCEAE (Muell. Arg.) Webster, Taxon 24: 600. 1975. Hippomaneae subtribe Stomatocalyceae Muell. Arg., Linnaea 34: 202. 1865. TYPE: *Stomatocalyx* Muell. Arg. [= *Pimelodendron* Hassk.].

Dioecious trees, shrubs, or lianas; latex yellowish, often scanty; indumentum usually absent; leaves alternate, unlobed, pinnately veined, without glands at base of blade; stipules small and caducous or absent. Inflorescences axillary, racemose, bracts eglandular. Staminate sepals 4–8, free and imbricate or connate and calyx 2-lipped; stamens 10–30, free, filaments short; pollen grains coarsely reticulate or reticulate-perforate. Pistillate sepals 5 or 6, free or connate and 2-lipped; ovary 2–10-locular; styles unlobed, sometimes dilated or stigmatiform. Fruit capsular or indehiscent, 1–3-seeded; seeds ecarunculate; endosperm copious, oily.

This tribe includes one neotropical and three paleotropical genera, distributed into two subtribes. Some characteristics within the Stomatocalyceae, such as the liana habit, colored latex, and oily endosperm, suggest possible affinity with *Omphalea*, in the Acalyphoideae.

KEY TO THE SUBTRIBES OF TRIBE STOMATOCALYCEAE

1a. Pollen grains finely reticulate-perforate; fruits indehiscent; styles abbreviated; ovary 2–10-locular ..... 45a. Stomatocalycinae
1b. Pollen grains coarsely reticulate; fruits capsular; styles ± elongated; ovary 2–3-locular ..... 45b. Hamilcoinae

45a. Subtribe STOMATOCALYCINAE Muell. Arg., Linnaea 34: 202. 1865; DC. Prodr. 15(2): 1142. 1866. TYPE: *Stomatocalyx* Muell. Arg. [= *Pimelodendron* Hassk.].

Trees or shrubs; leaves entire or dentate; racemes simple or slightly branched; sepals distinct or connate; stamens 10–20; pollen grains finely reticulate; ovary 1–10-locular; styles stigmatiform; fruit indehiscent, 1-seeded.

This subtribe includes two genera, one of Indonesia, the other of Africa.

KEY TO THE GENERA OF SUBTRIBE STOMATOCALYCINAE

1a. Sepals 6–8, free; ovary 1-locular ..... 272. *Plagiostyles*
1b. Sepals connate, staminate calyx 2-lipped; ovary 2–10-locular ..... 273. *Pimelodendron*

272. Plagiostyles Pierre, Bull. Mens. Soc. Linn. Paris 2: 1326. 1897; Prain, Kew Bull. 1912: 107. 1912; Fl. Trop. Afr. 6(1): 1001. 1913; Pax & Hoffm., Pflanzenr. 147. VII (Heft 63): 420. 1914; Stapf, Hook. Ic. Pl. 31: t. 3010. 1915; Léonard, Fl. Congo 8(1): 131. 1962. TYPE: *Plagiostyles klaineana* Pierre [= *Plagiostyles africana* (Muell. Arg.) Prain].

A monotypic genus of west Africa (southern Nigeria to Gabon and Congo).

273. Pimelodendron Hasskarl, Versl. Med. Afd. Natuurk. Kon. Akad. Wetensch. 4: 140. 1856; Benth., Gen. Pl. 3: 331. 1880; Pax & Hoffm., Pflanzenr. 147. V (Heft 52): 54. 1912; J. J. Smith, Bull. Jard. Bot. Buit. III. 6: 100. 1924; Whitmore, Tree Fl. Malaya 2: 124. 1973; Airy Shaw, Kew Bull. Add. Ser. 4: 186. 1975; 8: 196. 1980; Kew Bull. 36: 339. 1981. TYPE: *Pimelodendron amboinicum* Hassk.

Stomatocalyx Muell. Arg., DC. Prodr. 15(2): 1142. 1866. TYPE: *Stomatocalyx griffithianus* Muell. Arg. [= *Pimelodendron griffithianum* (Muell. Arg.) Benth. ex Hook. f.].

An Australasian genus of six to eight species distributed from Malaya to New Guinea, tropical Australia (Queensland), and the Solomon Islands.

45b. Subtribe HAMILCOINAE Pax & Hoffmann, Pflanzenr. 147. VII (Heft 63): 419. 1914. TYPE: *Hamilcoa* Prain.

Trees or lianas; leaves long-petiolate, entire or crenate; racemes simple or branched; staminate sepals 4 or 5, distinct, imbricate; stamens 10–20, free, filaments very short; pollen grains coarsely reticulate; pistillate sepals 4–6, ± distinct; ovary 2- or 3-locular; styles connate below, erect or spreading; fruit capsular.

A group of two genera, one American and one African. Although included in two different subtribes of the Gelonieae by Pax & Hoffmann (1931), *Hamilcoa* and *Nealchornea* share similar distinctively coarse-reticulate pollen grains that are curiously similar in ornamentation to those of *Dalechampia*.

KEY TO THE GENERA OF SUBTRIBE HAMILCOINAE

1a. Ovary 3-locular; styles erect; stamens 18–20; pistillate sepals not glandular; stems ± scandent ..... 274. *Hamilcoa*
1b. Ovary 2-locular; styles spreading; stamens 10; pistillate sepals with large basal glands; stems not scandent ..... 275. *Nealchornea*

274. Hamilcoa Prain, Kew Bull. 1912: 107. 1912; Fl. Trop. Afr. 6(1): 1000. 1913; Pax & Hoffm., Pflanzenr. 147. VII (Heft 63): 419. 1914; Stapf, Hook. Ic. Pl. 31: t. 3009. 1915; Keay, Fl. W. Trop. Afr., ed. 2, 1: 413. 1958. TYPE: *Hamilcoa zenkeri* (Pax) Prain [*Plukenetia zenkeri* Pax].

A monotypic genus of west African rainforests (Cameroon).

275. Nealchornea Huber, Bol. Mus. Goeldi 7: 297. 1913; Pax & Hoffm., Pflanzenr. 147. XIV (Heft 68): 51. 1919; Ducke, Arch. Jard. Bot. Rio de Janeiro 4: 107. 1925; Macbride, Field Mus. Nat. Hist., Bot. 13(IIIA, 1): 180. 1951. TYPE: *Nealchornea yapurensis* Huber.

A monotypic genus of the Amazonian rainforests (eastern Colombia and Peru to Brazil).

Tribe 46. HIPPOMANEAE A. Jussieu ex Spach, Hist. Nat. Veg. 2: 522. 1834. TYPE: *Hippomane* L.

Monoecious (less commonly dioecious) trees, shrubs, or herbs; latex usually milky, commonly acrid or toxic; indumentum simple or absent (dendritic in *Mabea*); leaves alternate (rarely opposite),

simple and unlobed, pinnately veined (rarely palmately veined), commonly with laminar or petiolar glands; stipules conspicuous to reduced or absent. Inflorescences terminal or axillary, racemose or spicate (sometimes paniculate), usually bisexual with one or a few pistillate flowers at base; bracts mostly glandular. Staminate calyx open in bud (exposing anthers), sepals distinct or connate, imbricate to valvate, sometimes vestigial or absent; stamens 1–70, free or filaments connate below; anthers discrete, exrorse; pollen grains 3-colporate, colpi usually marginate, sexine perforate-tectate. Pistillate sepals 3–6, imbricate, sometimes reduced or absent; ovary 2–3-locular (rarely 4–10); styles free or connate, unlobed. Fruit capsular or drupaceous; seeds carunculate or ecarunculate, testa dry or fleshy; endosperm copious, not markedly oily.

This diverse complex of 400–500 species was divided by Pax & Hoffmann (1912) into four subtribes, but these are so poorly defined that it seems impossible to maintain them. Generic delimitations are uncertain and controversial, and may change drastically when a monographic revision is completed.

KEY TO THE SUBTRIBES OF TRIBE HIPPOMANEAE

1a. Staminate receptacle convex or conical; staminate sepals 3–6, imbricate; stamens mostly 6–70, free; seeds carunculate; inflorescences terminal, paniculate; leaves stipulate, without petiolar glands ..... 46a. Mabeinae
1b. Staminate receptacle plane; staminate sepals mostly 2 or 3, sometimes only 1 or absent; stamens 1–6(–20), filaments free or united; inflorescences terminal or axillary, racemose or spicate (axes not compound); leaves often with petiolar glands.
2a. Staminate calyx laterally compressed; stamens 5–20, free; leaves with petiolar glands, stipules large and deciduous; latex watery; seeds carunculate ..... 46b. Carumbiinae
2b. Staminate calyx not laterally compressed; stamens 1–20, filaments free or connate; leaves with or without petiolar glands, stipules small or absent; latex usually milky; seeds carunculate or ecarunculate ..... 46c. Hippomaninae

Subtribe 46a. MABEINAE Pax & Hoffmann, Pflanzenr. 147. V (Heft 52): 22. 1912. TYPE: *Mabea* Aubl.

Monoecious trees or shrubs; latex milky, innocuous; indumentum of dendritic hairs, or absent; leaves alternate, pinnately veined, without laminar or petiolar glands, stipulate; inflorescences terminal, bisexual, racemose or paniculate, bracts biglandular; staminate sepals 3–6, imbricate; stamens 2–70, free from an expanded receptacle or connate into a column; pistillate sepals 3–6, sometimes glandular; ovary 3-locular, exappendiculate; styles connate into a column, tips slender and unlobed; fruit capsular; seeds carunculate.

This neotropical subtribe includes three genera as conventionally defined.

KEY TO THE GENERA OF SUBTRIBE MABEINAE

1a. Stylar column elongate; style tips slender, unlobed; inflorescence rachis ± flexuous; staminate flowers long-pedicellate; stamens (3–)10–70; leaves and stems with dendritic hairs ..... 276. *Mabea*
1b. Stylar column short, style tips rather thick; inflorescence rachis rigid; stamens 3–12.
2a. Latex very scanty or absent; indumentum absent; stamens 5–12; leaves chartaceous ..... 277. *Senefeldera*
2b. Latex copious, milky; indumentum of dendritic hairs present on inflorescence axes; stamens 2 or 3; leaves rigid ..... 278. *Senefelderopsis*

276. Mabea Aublet, Hist. Pl. Guyane Fr. 2: 867, t. 334. 1775; Muell. Arg., DC. Prodr. 15(2): 1148. 1866; Fl. Bras. 11(2): 515. 1874; Bentham, Gen. Pl. 3: 363. 1880; Pax & Hoffm., Pflanzenr. 147. V (Heft 52): 26. 1912; Jablonski, Mem. New York Bot. 17: 164. 1967; den Hollander & Berg, Proc. Kon. Ned. Akad. Wet. 89C: 147. 1986; Huft, Phytologia 62: 339. 1987; Ann. Missouri Bot. Gard. 75: 1125. 1989. TYPE: *Mabea piriri* Aubl. [lectotype, designated by Pfeiffer, Nomencl. Bot. 2(1): 191. 1874].

A diverse and difficult genus of ca. 50 neotropical species.

277. Senefeldera Martius, Flora 24 (Beibl. 2): 29. 1841; Muell. Arg., DC. Prodr. 15(2): 1153. 1866; Fl. Bras. 11(2): 529. 1874; Bentham, Gen. Pl. 3: 332. 1880; Pax & Hoffm., Pflanzenr. 147. V (Heft 52): 23. 1914; Jablonski, Mem. New York Bot. Gard. 12: 171. 1965; Webster, Ann. Missouri Bot. Gard. 75: 1127. 1989. TYPE: *Senefeldera multiflora* Mart.

A neotropical genus of 8–10 species, mainly in Amazonian South America but reaching north to Panama.

278. Senefelderopsis Steyermark, Bot. Mus. Leafl. Harvard Univ. 15: 45. 1951; Jablonski,

Mem. New York Bot. Gard. 12: 174. 1965; Gillespie, Brittonia 45: 92. 1993. TYPE: *Senefelderopsis croizatii* Steyerm.

A genus of four species endemic to South America (tepui areas of Colombia, Venezuela, northern Brazil).

Subtribe 46b. CARUMBIINAE Muell. Arg., Linnaea 34: 203. 1865; DC. Prodr. 15(2): 1142. 1866. TYPE: *Carumbium* Reinw. [= *Omalanthus* A. Juss.].

Hippomaneae subtribe Homalanthinae Pax & Hoffm., Pflanzenr. 147. V (Heft 52): 42. 1912. TYPE: *Omalanthus* A. Juss.

Monoecious or dioecious trees or shrubs; latex watery, innocuous; leaves entire, pinnately to palmately veined, petiolate, glandular at apex of petiole, stipulate; inflorescence terminal, racemose, usually bisexual, bracts biglandular; staminate calyx compressed and 2-lipped, or of only 1 lobe; stamens 5–50, filaments free; pistillate calyx 2- or 3-lobed; ovary 2-locular (rarely 3-locular), exappendiculate; styles free or nearly so, unlobed to bifid, usually glandular near tip; fruit dehiscent or indehiscent; seeds with large caruncle.

As interpreted earlier (Webster, 1975), subtribe Carumbiinae is here treated as including only the type genus *Omalanthus*. Pax & Hoffmann (1912) also included *Pimelodendron* in the subtribe, probably because of the similar staminate calyx. However, *Pimelodendron* differs in its pollen sexine ornamentation, eglandular bracts, and ecaruncullate seeds.

279. Omalanthus A. Jussieu, Tent. Euphorb. 50. 1824; Bentham, Gen. Pl. 3: 331. 1880 (as *Homalanthus*); Pax & Hoffm., Pflanzenr. 147. V (Heft 52): 42. 1912; J. J. Smith, Nova Guinea 8: t. 140, 141. 1912; 12: t. 228, 229. 1917; Airy Shaw, Kew Bull. 21: 409. 1968; Kew Bull. Add. Ser. 8: 115. 1980; Sykes, New Zeal. J. Bot. 7: 302. 1969; A. C. Smith, Fl. Vit. Nova 2: 558. 1981; St. John, Nordic J. Bot. 4: 53. 1984. TYPE: *Omalanthus leschenaultianus* A. Juss. [= *Omalanthus populneus* (Geisel.) Pax].

Carumbium Reinwardt, Syll. Pl. Nov. 2(1): 6. 1826. TYPE: *Carumbium populifolium* Reinw. [= *Omalanthus populneus* (Geisel.) Pax].

Wartmannia Muell. Arg., Linnaea 34: 218. 1865. TYPE: *Wartmannia stillingiifolia* (F. Muell.) Muell. Arg. [= *Omalanthus stillingiifolius* F. Muell.].

Dibrachion Regel, Index Sem. Hort. Bot. Petropol. 1865: 51. 1866. TYPE: *Dibrachion peltatum* Regel [= *Omalanthus fastuosus* (Linden) Villar].

An Old World genus of ca. 30 species, extending from Malaya through Indonesia to the Pacific islands (as far as Tahiti and the Austral Islands).

Subtribe 46c. HIPPOMANINAE Grisebach, Fl. Brit. W. Ind. 49. 1859; Pax, Natürl. Pflanzenfam. ed. 1, 3(5): 91. 1890. TYPE: *Hippomane* L.

Hippomaneae subtribe Adenopeltinae Pax & Hoffm., Pflanzenr. 147. V. (Heft 52): 57. 1912. TYPE: *Adenopeltis* Bert.

Hippomaneae subtribe Excoecariinae Pax & Hoffm., Pflanzenr. 147. V (Heft 52): 153. 1912. TYPE: *Excoecaria* L.

Hippomaneae subtribe Gymnanthinae Pax & Hoffm., Pflanzenr. 147. V (Heft 52): 57. 1912. TYPE: *Gymnanthes* Sw.

Hippomaneae subtribe Stillingiinae Pax & Hoffm., Pflanzenr. 147. V (Heft 52): 174. 1912. TYPE: *Stillingia* Garden ex L.

Monoecious or dioecious trees, shrubs, or herbs; latex milky, often caustic; indumentum simple or absent; leaves alternate (rarely opposite), usually unlobed, pinnately veined, often with laminar or petiolar glands; stipules mostly small, sometimes obsolete or absent; inflorescences terminal or axillary, mostly spicate (sometimes racemose), bracts usually biglandular; staminate calyx open in bud, sepals 0–3; stamens 1–20, free or connate; pistillate sepals mostly 2 or 3, sometimes obsolete or absent; ovary 2–4-locular (6–10-locular in *Hippomane*), often carinate or horned; styles ± connate, unlobed; fruit capsular or drupaceous; seeds carunculate or ecarunculate.

This subtribe is the major taxon within the subfamily other than the tribe Euphorbieae. The 500-odd species are distributed among about 15 genera, many of which are notoriously poorly delimited. Pax & Hoffmann (1912) proposed an unworkable system in which the genera were assigned to five subtribes; these cannot be satisfactorily distinguished. Future monographic work may provide some clues that will make it possible to subdivide subtribe Hippomaninae, but at present, a subdivision seems premature.

KEY TO THE GENERA OF SUBTRIBE HIPPOMANINAE

1a. Ovary 2–3-locular; fruits capsular or drupaceous.
2a. Staminate spikes not capitular (or if so, seeds not foveolate).

3a. Staminate spikes conspicuously bracteate; staminate sepals mostly 3–5; stamens 3; seeds ecarunculate ..... 280. *Spirostachys*
3b. Staminate spikes usually not conspicuously bracteate; staminate sepals 2 or 3 (or obsolete).
4a. Seeds generally carunculate, testa dry.
5a. Spikes usually terminal or opposite leaves; staminate calyx 2–3-lobed; pistillate flowers sessile or short-pedicellate (fruiting pedicels less than 1 cm long).
6a. Columella not 3-horned at base; pistillate flowers often pedicellate ..... 281. *Sebastiania*
6b. Columella 3-horned at base; pistillate flowers sessile ..... 282. *Stillingia*
5b. Spikes axillary; staminate sepals 1 or 2, often reduced or obsolete; pistillate flowers distinctly pedicellate (1 cm long or more in fruit) ..... 283. *Gymnanthes*
4b. Seeds generally ecarunculate, testa dry or fleshy.
7a. Fruit capsular (or if drupaceous then bracts glandular).
8a. Dioecious (rarely monoecious); petioles usually eglandular; inflorescences axillary; staminate sepals distinct; ovary not appendiculate; caruncle deciduous from seed and persistent on columella ..... 284. *Excoecaria*
8b. Monoecious; petioles often glandular; inflorescences terminal or axillary.
9a. Bracts glandular; leaves mostly with petiolar glands.
10a. Seed coat dry; calyx suppressed.
11a. Columella not 3-horned.
12a. Stamens 2–4; leaves pinnately veined, unlobed ..... 285. *Colliguaja*
12b. Stamen 1; leaves palmately veined, ± lobed ..... 286. *Dalembertia*
11b. Columella 3-horned; leaves pinnately veined ..... 287. *Adenopeltis*
10b. Seed coat fleshy; staminate calyx present ..... 288. *Sapium*
9b. Bracts eglandular.
13a. Spikes capitular, pseudoaxillary; stamens 3, filaments exserted beyond gamophyllous calyx; styles connate ..... 289. *Glyphostylus*
13b. Spikes elongated.
14a. Spikes terminal; filaments connate; leaves with glands at apex of petiole ..... 290. *Grimmeodendron*
14b. Spikes axillary; filaments free; leaves eglandular ..... 291. *Bonania*
7b. Fruit drupaceous; inflorescences axillary; bracts eglandular ..... 292. *Duvigneaudia*
2b. Staminate spikes capitular, terminal; bracts glandular; seeds foveolate, with large caruncle ..... 293. *Maprounea*
1b. Ovary 6–10-locular; fruits drupaceous; spikes terminal; bracts glandular ..... 294. *Hippomane*

280. Spirostachys Sonder, Linnaea 23: 106. 1850; Pax & Hoffm., Pflanzenr. 147. V (Heft 52): 153. 1912; Prain, Fl. Trop. Afr. 6(1): 1005. 1913; Alfaro Cardoso, Serv. Agric. Moçamb., Publ. A18: 1. 1964; Dyer, Gen. S. Afr. Fl. Pl. ed. 3, 322. 1975; Radcliffe-Smith, Fl. E. Trop. Afr., Euphorb. 1: 385. 1987. TYPE: *Spirostachys africana* Sond.

An African genus of one species (or two, if *Excoecaria venenifera* Pax is included).

281. Sebastiania Sprengel, Neue Entdeck. Pflanzenk. 2: 118, t. 3. 1820; Muell. Arg., DC. Prodr. 15(2): 1164. 1866; Fl. Bras. 11(2): 544. 1874; Bentham, Gen. Pl. 3: 336. 1880; Pax & Hoffm., Pflanzenr. 147. V (Heft 52): 88. 1914; Natürl. Pflanzenfam. ed. 2, 19c: 192. 1931; Smith, Downs & Klein, Fl. Illustr. Catar. EUFO 242. 1988; Webster & Huft, Ann. Missouri Bot. Gard. 75: 1127. 1989. TYPE: *Sebastiania brasiliensis* Spreng.

Gussonia Sprengel, Neue Entdeck. Pflanzenk. 2: 119. 1820. TYPE: *Gussonia discolor* Spreng. [= *Sebastiania discolor* (Spreng.) Muell. Arg.].

Microstachys A. Jussieu, Euphorb. Tent. 48. 1824. TYPE: *Microstachys bicornis* (Vahl) A. Juss. [= *Sebastiania corniculata* (Vahl) Muell. Arg.; lectotype].

Cnemidostachys Martius & Zuccarini, Nova Gen. Sp. 1: 66. 1824. TYPE: not designated (Martius described a large number of taxa of *Cnemidostachys*, and the choice of lectotype is best left to a future monographer of this group).

Ditrysinia Raf., Neogenyton 2. 1825. TYPE: *Ditrysinia ligustrina* (Mx.) Raf. [= *Sebastiania ligustrina* Mx.].

Adenogyne Klotzsch, Arch. Naturgesch. 7: 183. 1841. TYPE: *Adenogyne pachystachya* Kl. [= *Sebastiania pachystachys* (Kl.) Muell. Arg.].

Sarothrostachys Klotzsch, Arch. Naturgesch. 7: 185. 1841. TYPE: *Gymnanthes multiramea* Baillon [= *Sebastiania multiramea* (Baillon) Muell. Arg.].

Elachocroton F. Mueller, Hook. J. Bot. Kew Gard. Misc. 9: 17. 1857. TYPE: *Elachocroton asperococcum* F. Muell. [= *Sebastiania chamaelea* (L.) Muell. Arg.].

Tragiopsis Karsten, Wochenschr. Gaertnerei Pflanzenk. 2: 5. 1859. TYPE: *Tragiopsis fruticulosa* Karst. [= *Sebastiania corniculata* (Vahl) Muell. Arg.].

Dendrocousinsia Millspaugh, Field Mus. Publ. Bot. 2: 374. 1913. TYPE: *Dendrocousinsia spicata* Millsp. [= *Sebastiania spicata* (Millsp.) Pax & Hoffm.].

A genus of ca. 100 species, mainly neotropical, but with outliers in temperate North America, Asia, and Australasia. The herbaceous species of section

Microstachys appear very different from the woody ones and may possibly represent a distinct genus. However, there are connecting links such as *Sebastiania panamensis* Webster (Webster & Huft, 1988), so that it seems preferable at present to maintain the broad (and probably unnatural) generic circumscription of Pax & Hoffmann (1931).

282. Stillingia Garden ex L., Syst. Nat. ed. 12, 2: 637. 1767; Mant. Pl. 19, 126. 1767; Muell. Arg., DC. Prodr. 15(2): 1155. 1866; Fl. Bras. 11(2): 537. 1874; Bentham, Gen. Pl. 3: 334. 1880; Pax & Hoffm., Pflanzenr. 146. V (Heft 52): 180. 1912; Rogers, Ann. Missouri Bot. Gard. 38: 207. 1951; van Steenis, Blumea Suppl. 5: 302. 1966; Webster, J. Arnold Arbor. 48: 388. 1967; A. C. Smith, Fl. Vit. Nov. 2: 565. 1981. TYPE: *Stillingia sylvatica* L.

Gymnostillingia Muell. Arg., Linnaea 32: 89. 1863. TYPE: *Gymnostillingia acutifolia* (Benth.) Muell. Arg. [= *Stillingia acutifolia* (Benth.) Hemsl.; lectotype, designated by Wheeler, 1975].

A mainly American genus of ca. 25 species, with a few disjunct taxa in the Mascarene Islands, eastern Malaysia, and Fiji.

283. Gymnanthes Swartz, Prodr. Veg. Ind. Occ. 6, 95. 1788; Grisebach, Fl. Brit. W. Ind. 50. 1859; Bentham, Gen. Pl. 3: 337. 1880; Sargent, Silva N. Amer. 7: t. 309. 1895; Pax & Hoffm., Pflanzenr. 147. V. (Heft 52): 81. 1912; Fawc. & Rend., Fl. Jam. 4: 329. 1920; Webster, J. Arnold Arbor. 48: 387. 1967; Taxon 32: 304. 1983; Ann. Missouri Bot. Gard. 75: 1129. 1989. TYPE: *Gymnanthes lucida* Sw. [lectotype, chosen by Grisebach, 1859].

Actinostemon Martius ex Klotzsch, Arch. Naturgesch. 7: 184. 1841; Pax & Hoffm., Pflanzenr. 147. V (Heft 52): 57. 1912; Jablonski, Phytologia 18: 213. 1969. TYPE: *Actinostemon concolor* (Spreng.) Muell. Arg. [*Gussonia concolor* Spreng. = *Gymnanthes concolor* (Spreng.) Muell. Arg.; lectotype, designated by Jablonski, Mem. New York Bot. Gard. 17: 177. 1967; Farr et al. (1979) incorrectly cited *Actinostemon grandifolius* Kl., an invalid name].

Dactylostemon Klotzsch, Arch. Naturgesch. 7: 181. 1841. TYPE: *Dactylostemon schomburgkii* Kl., Hook. London J. Bot. 2: 44. 1843 [= **Gymnanthes schomburgkii** (Kl.) Webster, comb. nov.; lectotype, chosen here].

As circumscribed here following Webster (1989), *Gymnanthes* is an American genus of ca. 40 species. Although most 20th-century workers have followed Pax & Hoffmann (1912) in recognizing *Actinostemon* as a distinct genus, there appear to be no satisfactory distinguishing characters. In the previous century, Baillon (1858) upheld *Actinostemon* as distinct, while Mueller (1866) maintained *Actinostemon* and *Dactylostemon* as separate genera but combined *Gymnanthes* with *Sebastiania*. Generic delimitation clearly remains a major problem in this complex of neotropical Hippomaninae with reduced staminate flowers.

Following Rothmaler (1944), a number of American botanists have adopted the name *Ateramnus* P. Browne in place of *Gymnanthes*. However, this is based on a very questionable identification of Browne's plant from Jamaica with *Gymnanthes lucida* Sw.; it appears more likely that Browne had a species of *Sapium* (Webster, 1983).

284. Excoecaria L., Syst. Nat. ed. 10, 1288. 1759; Bentham, Gen. Pl. 3: 337. 1880; Hook. f., Fl. Brit. Ind. 5: 472. 1888; Pax & Hoffm., Pflanzenr. 147. V (Heft 52): 157. 1912; Gagnepain, Fl. Indochine 5: 402. 1926; Airy Shaw, Kew Bull. 26: 268. 1971; Whitmore, Tree Fl. Malaya 2: 96. 1973; Airy Shaw, Kew Bull. Add. Ser. 4: 112. 1975; 8: 88. 1980; Kew Bull. 35: 630. 1980; 36: 296. 1981; Radcliffe-Smith, Fl. E. Trop. Afr. Euphorb. 1: 382. 1987. TYPE: *Excoecaria agallocha* L.

Commia Loureiro, Fl. Cochinchin. 605. 1790. TYPE: *Commia cochinchinensis* Lour. [= *Excoecaria agallocha* L. ?].

Anomostachys (Baillon) Hurusawa, J. Fac. Sci. Univ. Tokyo Bot. 6: 311. 1954. TYPE: *Stillingia lastellii* Baillon [= *Excoecaria lastellii* (Baillon) Muell. Arg.].

A paleotropical genus of ca. 40 species, mostly in tropical Asia but a few taxa in Africa, Madagascar, and tropical Australia. Mueller (1866, 1874) gave *Excoecaria* a very broad circumscription including *Sapium*, but this has not been followed by recent authors.

285. Colliguaja Molina, Saggio Chile 158. 1781; Hooker, Bot. Misc. 1: 138. 1830; Muell. Arg., DC. Prodr. 15(2): 1226. 1866; Fl. Bras. 11(2): 630, t. 85. 1874; Bentham, Gen. Pl. 3: 338. 1880; Pax & Hoffm., Plfanzenr. 147. V (Heft 52): 265. 1912; L. Smith et al., Fl. Illustr. Catar. EUFO 326. 1988. TYPE: *Colliguaja odorifera* Mol.

A South American genus of five species.

286. Dalembertia Baillon, Etude Gén. Euphorb. 545. 1858; Muell. Arg., DC. Prodr. 15(2): 1225. 1866; Bentham, Gen. Pl. 3:

339. 1880; Pax & Hoffm., Pflanzenr. 147. V (Heft 52): 268. 1912; Standley & Steyerm., Fieldiana Bot. 24(6): 86. 1949. TYPE: *Dalembertia populifolia* Baillon.

Alcoceria Fernald, Proc. Amer. Acad. Arts Sci. 36: 493. 1901. TYPE: *Alcoceria pringlei* Fern. [= *Dalembertia populifolia* Baillon].

A well-marked genus of five species in Mexico and Guatemala, distinguished by its compact inflorescence and highly reduced staminate flowers.

287. Adenopeltis Bertero ex A. Jussieu, Ann. Sci. Nat. I. 25: 24. 1832; Muell. Arg., DC. Prodr. 15(2): 1164. 1866; Bentham, Gen. Pl. 3: 338. 1880; Pax & Hoffm., Pflanzenr. 147. V (Heft 52): 264. 1912. TYPE: *Adenopeltis colliguaya* Bert. ex A. Juss. (nom. illeg.) [= *Excoecaria serrata* Ait., Hort, Kew. ed. 2, 5: 418. 1813; = **Adenopeltis serrata** (Ait.) Webster, comb. nov.].

A monotypic genus of Chile.

288. Sapium P. Browne, Civ. Nat. Hist. Jam. 338. 1756; Jacquin, Select. Stirp. Amer. Hist. 249. 1763; Bentham, Gen. Pl. 3: 334. 1880; Hemsley, Hook. Ic. Pl. 27: t. 2647–2650, 2677–2684. 1901–1902; 29: t. 2878–2900. 1909; Pittier, Contr. U.S. Natl. Herb. 12: 159. 1906; Pax & Hoffm., Pflanzenr. 147. V (Heft 52): 199. 1912; Fawc. & Rend., Fl. Jam. 4: 324. 1920; Gagnepain, Fl. Indochine 5: 394. 1926; Léonard, Bull. Jard. Bot. Brux. 29: 133. 1959; Fl. Congo 8(1): 151. 1962; Webster, J. Arnold Arbor. 48: 391. 1967; Jablonski, Phytologia 14: 441. 1967; 16: 393. 1968; Radcliffe-Smith, Fl. E. Trop. Afr., Euphorb. 1: 389. 1987; Huft, Ann. Missouri Bot. Gard. 75: 1132. 1989; Kruijt & Zijlstra, Taxon 38: 320. 1989. TYPE: *Sapium jamaicense* Sw.

Triadica Loureiro, Fl. Cochinchin. 610. 1790. TYPE: *Triadica sinensis* Lour. [= *Sapium sebiferum* (L.) Roxb.; lectotype, chosen here].

Falconeria Royle, Ill. Bot. Himal. 354. 1839. TYPE: *Falconeria insignis* Royle [= *Sapium insigne* (Royle) Benth.; lectotype, designated by Wheeler, Taxon 24: 535].

Conosapium Muell. Arg., Linnaea 32: 87. 1863. TYPE: *Conosapium madagascariense* Muell. Arg. [= *Sapium madagascariense* (Muell. Arg.) Pax].

Taeniosapium Muell. Arg., DC. Prodr. 15(2): 1200. 1866. TYPE: *Taeniosapium goudotianum* (Muell. Arg.) Muell. Arg. [= *Sapium goudotianum* (Muell. Arg.) Pax].

Shirakia Hurusawa, J. Fac. Sci. Univ. Tokyo, Bot. 6: 317. 1954. TYPE: *Shirakia japonica* (Sieb. & Zucc.) Hurus. [= *Sapium japonicum* (Sieb. & Zucc.) Pax].

As here delimited, *Sapium* is a large and diverse genus of ca. 90–100 species, the majority neotropical, a minority Asian. *Triadica*, accepted by some Asian workers, is distinctively different from the neotropical species in such features as its nonarillate seeds; further investigation may show that it should be generically separate from *Sapium*.

289. Glyphostylus Gagnepain, Bull. Soc. Bot. France 71: 871. 1925; Fl. Indochine 5: 402. 1926; Airy Shaw, Kew Bull. 16: 372. 1963; 26: 281. 1972. TYPE: *Glyphostylus laoticus* Gagnep.

A monotypic genus of southeast Asia (Thailand to Vietnam).

290. Grimmeodendron Urban, Symb. Ant. 5: 397. 1908; Pax & Hoffm., Pflanzenr. 147. V (Heft 52): 258. 1912; Fawc. & Rend., Fl. Jam. 4: 326. 1920; Alain, Fl. Cuba 3: 119. 1953; Correll & Correll, Fl. Bahama Arch. 818. 1982; Liogier, Fl. Española 4: 153. 1986: TYPE: *Grimmeodendron jamaicense* Urban [lectotype, designated by Wheeler, 1975].

A West Indian genus of two species.

291. Bonania A. Richard, Hist. Fis. Cuba, 2, 11: 201. 1853; Bentham, Gen. Pl. 3: 335. 1880; Pax & Hoffm., Pflanzenr. 147. V (Heft 52): 259. 1912; Alain, Fl. Cuba 3: 115. 1953; Borhidi, Acta Bot. Acad. Sci. Hungar. 22: 305. 1976; Correll & Correll, Fl. Bahama Arch. 784. 1982. TYPE: *Bonania cubana* A. Rich.

Hypocoton Urban, Symb. Ant. 7: 263. 1912. TYPE: *Hypocoton domingensis* Urb. [= *Bonania domingensis* (Urb.) Urb.].

A genus of ca. eight species, mostly in Cuba but with one each in the Bahamas and Hispaniola.

292. Duvigneaudia Léonard, Bull. Jard. Bot. Brux. 29: 15. 1959; Fl. Congo 8(1): 139. 1962. TYPE: *Duvigneaudia inopinata* (Prain) Léonard.

A monotypic genus of west Africa (Cameroon to Congo and Gabon).

293. Maprounea Aublet, Hist. Pl. Guiane Fr. 895. 1775; Muell. Arg., DC. Prodr. 15(2):

1190. 1866; Fl. Bras. 11(2): 542. 1874; Bentham, Gen. Pl. 3: 333. 1880; Pax & Hoffm., Pflanzenr. 147. V (Heft 52): 175. 1912; Léonard, Fl. Congo 8(1): 142. 1962; Radcliffe-Smith, Fl. E. Trop. Afr. Euphorb. 1: 395. 1987; Webster, Ann. Missouri Bot. Gard. 75: 1131. 1988; L. Smith et al., Fl. Illustr. Catar. EUFO 316. 1988. TYPE: *Maprounea guianensis* Aubl.

Aegopricum L., Pl. Surinam. 15. 1775. TYPE: *Aegopricum betulinum* L. [= *Maprounea guianensis* Aubl.].

A genus with a disjunct distribution, one or two species in South America and Panama, and two in west Africa.

294. Hippomane L., Sp. Pl. 1191. 1753; Gen. Pl. 499. 1754; Muell. Arg., DC. Prodr. 15(2): 1199. 1866; Bentham, Gen. Pl. 3: 333. 1880; Pax & Hoffm., Pflanzenr. 147. V (Heft 52): 261. 1912; Fawc. & Rend., Fl. Jam. 4: 327. 1920; Webster, J. Arnold Arbor. 48: 393. 1967; Correll & Correll, Fl. Bahama Arch. 818. 1982; Liogier, Fl. Española 4: 158. 1986; Webster, Ann. Missouri Bot. Gard. 75: 1131. 1988; Howard, Fl. Lesser Ant. 5: 54. 1989. *Mancanilla* Miller, Gard. Dict. Abr. Ed. 4. 1754. TYPE: *Hippomane mancinella* L. [lectotype, designated by M. L. Green, Prop. Brit. Bot. 195. 1929].

A neotropical genus of three species, one widespread in the Caribbean and Galápagos, the other two endemic to Hispaniola.

Tribe 47. PACHYSTROMATEAE (Pax & Hoffmann) Pax, Bot. Jahrb. 59: 145. 1924. Acalypheae subtribe Pachystromatinae Pax & Hoffm., Pflanzenr. 147. XIV (Heft 68): 3. 1919. TYPE: *Pachystroma* Muell. Arg.

Monoecious trees or shrubs; stems with milky latex; indumentum absent; leaves alternate, unlobed, pinnately veined, margins entire to mostly spinose-dentate, stipulate. Inflorescence spicate, terminal, pistillate flowers proximal on spikes or in upper axils; staminate bracts biglandular. Staminate flowers subsessile; sepals 5 or 6, valvate; disk absent; stamens 3, filaments connate into a column, anthers extrorse; pollen grains 3-colporate, perforate-tectate; pistillode absent. Pistillate flowers subsessile; sepals 3, persistent; disk absent; ovary 3-locular; styles basally connate, unlobed. Fruit capsular; columella 3-horned at base; seeds ecaruncula te, endosperm present.

This tribe includes only the type genus *Pachystroma*. The position of this tribe has been poorly understood owing to its initial misplacement by Mueller (1866) in the Acalypheae because of the valvate staminate calyx. Bentham, apparently misled by Mueller, referred *Pachystroma* to his subtribe Adrianeae. Pax & Hoffmann (1919) followed Mueller's example by creating a subtribe Pachystrominae in the Acalphyeae, and finally (Pax, 1924; Pax & Hoffmann, 1931) placed the genus in a separate tribe following the Acalphyeae. Curiously, no one seems to have paid attention to the opinion of Baillon (1865, 1866), who placed his synonymous genus *Acantholoma* in the Hippomaneae in the vicinity of *Stillingia*. In support of Baillon's disposition, characters such as the laticiferous stems, spicate inflorescence with glandular bracts, and perforate-tectate pollen grains of *Pachystroma* clearly rule out a placement in the Acalyphoideae and indicate a position in the Euphorbioideae. In fact, it is rather doubtful that *Pachystroma* should be kept in a distinct tribe; further study will probably show that it should be referred to a subtribe of the Hippomaneae.

295. Pachystroma Muell. Arg., Linnaea 34: 177. 1865; DC. Prodr. 15(2): 893. 1866; Fl. Bras. 11(2): 387, t. 54. 1874; Bentham, Gen. Pl. 3: 307. 1880; Pax, Pflanzenr. 147. II (Heft 44): 99. 1910; Pax & Hoffm., Natürl. Pflanzenfam. ed. 2, 19c: 151. 1931; Smith et al., Fl. Ilustr. Catar. EUFO 225. 1988. TYPE: *Pachystroma ilicifolium* Muell. Arg. [= *Pachystroma longifolium* (Nees) I. M. Jhnt.].

Acantholoma Gaudichaud ex Baillon, Adansonia I. 6: 231. 1866. TYPE: *Acantholoma spinosum* Gaud. ex Baillon [= *Pachystroma longifolium* (Nees) I. M. Jhnt.].

This monotypic Brazilian genus includes a single variable species found from Minas Gerais to Rio Grande do Sul.

Tribe 48. HUREAE Dumortier, Anal. Fam. Pl. 45. 1829 (as Huraceae); Webster, Taxon 24: 600. 1975. Hippomaneae subtribe Hureae Muell. Arg., Linnaea 34: 203. 1865. TYPE: *Hura* L.

Monoecious trees or shrubs; latex ± toxic; indumentum absent; leaves alternate, unlobed, pinnately veined, biglandular at base of blade, stipulate. Inflorescences terminal or axillary, spicate. bracts ± adnate to rachis of inflorescence, eglandular. Staminal calyx 2–3-lobed; disk absent; sta-

mens 1–20, free or filaments connate; pollen grains 3-colporate, colpi somewhat marginate, sexine very finely perforate-tectate. Pistillate sepals 5 or 6, free or connate; ovary 3–20-locular, exappendiculate; styles unlobed, connate. Fruit capsular; seeds ecarunculate, testa dry.

This strictly American tribe of four genera, with its center of diversity in eastern Brazil, closely approaches the tribe Hippomaneae via *Dalembertia*.

KEY TO THE GENERA OF TRIBE HUREAE

1a. Sepals 3–5, imbricate; styles united halfway or less.
  2a. Filaments of stamens connate; styles connate less than halfway; petioles mostly 1 cm or longer ..... 296. *Tetraplandra*
  2b. Filaments free; styles connate halfway or more; petioles mostly 1 cm or shorter ..... 297. *Algernonia*
1b. Sepals not imbricate; styles completely connate into a long column.
  3a. Ovary 3-locular; stylar column apically 3-lobed; stamen 1; staminate calyx rupturing into 2 or 3 segments; inflorescences axillary; leaves oblanceolate, cuneate at base ..... 298. *Ophthalmoblapton*
  3b. Ovary 5–20-locular; stylar column apically dilated into a lobed disk; stamens 10–80, filaments connate; staminate calyx cupulate, truncate; inflorescences terminal (or pistillate flowers axillary); leaves ovate, rounded to cordate at base ..... 299. *Hura*

296. Tetraplandra Baillon, Ann. Sci. Nat. IV. 9: 200. 1858; Etude Gén. Euphorb. 549. 1858; Muell. Arg., DC. Prodr. 15(2): 1230. 1866; Fl. Bras. 11(2): 533. 1874; Pax & Hoffm., Pflanzenr. 147. V (Heft 52): 275. 1912; Emmerich, Arq. Mus. Nac. Rio de Janeiro 56: 94. 1981. TYPE: *Tetraplandra leandri* Baill.

A neotropical genus of seven species, mostly in eastern Brazil, but also recorded from the Amazonian region as far west as Peru (Huft, pers. comm.).

297. Algernonia Baillon, Ann. Sci. Nat. IV. 9: 198. 1858; Etude Gén. Euphorb. 546. 1858; Muell. Arg. 15(2): 1230. 1866; Bentham, Gen. Pl. 3: 339. 1880; Pax & Hoffm., Pflanzenr. 147. V (Heft 52): 276. 1912; Emmerich, Arq. Mus. Nac. Rio de Janeiro 56: 92. 1981; Bradea 3: 148. 1981. TYPE: *Algernonia brasiliensis* Baill.

A neotropical genus of five species, endemic to eastern Brazil. The genera *Algernonia* and *Tetraplandra* appear very closely related, and it might be preferable to treat them as subgenera of a single genus.

298. Ophthalmoblapton Fr. Allemão, Pl. Novas Brasil, 1849; Ann. Sci. Nat. Bot. III. 13: 119. 1849; Muell. Arg. 15(2): 1155. 1866; Fl. Bras. 11(2): 531. 1874; Bentham, Gen. Pl. 3: 333. 1880; Pax & Hoffm., Pflanzenr. 147. V. (Heft 52): 278. 1912; Emmerich, Bol. Mus. Nac. Rio de Janeiro, Bot. 62: 1. 1981; L. Smith et al., Fl. Illustr. Catar. EUFO 325. 1988; Howard, Fl. Lesser Ant. 5: 57. 1989. TYPE: *Ophthalmoblapton* Fr. Allem.

A neotropical genus of four species endemic to eastern Brazil.

299. Hura L., Sp. Pl. 1008. 1753; Gen. Pl. ed. 5, 439. 1754; Muell. Arg., DC. Prodr. 15(2): 1228. 1866; Bentham, Gen. Pl. 3: 339. 1880; Pax & Hoffm., Pflanzenr. 147. V (Heft 52): 271. 1912; Fawc. & Rend., Fl. Jam. 4: 333. 1920; Standley & Steyerm., Fieldiana Bot. 24(6): 124. 1949; Burch, Ann. Missouri Bot. Gard. 54: 330. 1968; Correll & Correll, Fl. Bahama Arch. 821. 1982. TYPE: *Hura crepitans* L.

A neotropical genus of two species, the type widespread from Cuba and Mexico south to Brazil, the other (*H. polyandra* Baill.) recorded from Mexico to Costa Rica; widely introduced throughout the tropics.

Tribe 49. EUPHORBIEAE [Blume, Bijdr. 631. 1825]; Pax & Hoffmann, Natürl. Pflanzenfam. ed. 2, 19c: 207. 1931; Wheeler, Amer. Midl. Nat. 30: 477. 1943. TYPE: *Euphorbia* L.

Monoecious (or less commonly dioecious) trees, shrubs, or herbs; latex milky, innocuous or toxic; indumentum simple or absent; leaves alternate, opposite, or whorled, mostly unlobed and pinnately veined, without laminar or petiolar glands; stipules present or absent. Inflorescences pseudanthial, the connate bracts forming a cyathium enclosing a single terminal pistillate flower and 4 or 5 lateral staminate monochasia; bracts eglandular. Staminate flower with calyx reduced or absent; stamen 1; pollen grains 3-colporate, colpi marginate, sexine perforate-tectate. Pistillate flower with calyx

3–6-lobed or absent; ovary (2-)3-(4-)locular; styles free or basally connate, bifid (rarely entire). Fruit capsular (rarely drupaceous); seeds carunculate or ecarunculate; testa dry, smooth or ornamented.

A large tribe of more than 1500 species, here divided (following Webster, 1975) into 3 subtribes with 11 genera. A catalogue of the more than 2000 species names in tribe Euphorbieae has recently been published by Oudejans (1990).

KEY TO THE SUBTRIBES OF TRIBE EUPHORBIEAE

1a. Staminate calyx present; involucre of 4 bracts, partially fused; cyathial glands commissural, not on rim of cyathial tube ..... 49a. Anthosteminae
1b. Staminate calyx absent; involucral bracts usually 5, connate into a tube.
  2a. Petaloid appendages bracteal (dilated involucral lobes), opposite the staminate monochasia; cyathial glands commissural; bracts of staminate monochasia large, imbricate, enclosing staminate flowers; pistillate sepals 5 or 6, large, imbricate ..... 49b. Neoguillauminiinae
  2b. Petaloid appendages interbracteal (i.e., opposite cyathial glands), alternate with staminate monochasia (sometimes absent); cyathial glands on rim of cyathium; bracts of staminate monochasia small or obsolete ..... 49c. Euphorbiinae

Subtribe 49a. ANTHOSTEMINAE (Baillon) Webster, Taxon 24: 600. 1975. Anthostemideae Baillon, Ann. Sci. Nat. IV. 9: 192. 1858. Anthostemeae Kl. & Gcke., Monatsber. Königl. Preuss. Akad. Wiss. Berlin 1859: 247. 1859. TYPE: *Anthostema* A. Juss.

Monoecious or dioecious trees; leaves alternate, pinnately veined, stipules inconspicuous; cyathia in terminal or axillary dichasia; cyathial involucre of 4 outer bracts subtending or enclosing 4 subflorescences; pistillate flower solitary, central and terminal (or apparently lateral); staminate flowers in dichasia ± enclosed by 4 secondary (inner) bracts; cyathial glands projecting inward from infolded margins of outer bracts; staminate flowers and pistillate flowers with gamophyllous calyx; ovary 3–4-locular; styles emarginate to bifid; fruit capsular; seeds carunculate or ecarunculate.

This paleotropical subtribe includes two genera of Africa and Madagascar. The cyathia in the Anthosteminae are apparently tetramerous and somewhat bilaterally symmetrical; the tetramery carries over to some extent in the Neoguillauminiinae, suggesting that the pentamerous condition in the Euphorbiinae may be a derived condition.

KEY TO THE GENERA OF SUBTRIBE ANTHOSTEMINAE

1a. Cyathia bisexual; involucral bracts laterally connate into an open 4-lobed involucre; cyathial glands at margins of internal bracts; inflorescences axillary; ovary 3-locular. 300. *Anthostema*
1b. Cyathia mostly unisexual; outer involucral bracts connate into a closed tube; cyathial glands fused by pairs into 4 lobes alternating with involucral lobes; inflorescences terminal; ovary 4-locular ..... 301. *Dichostemma*

300. Anthostema A. Jussieu, Euphorb. Tent. 56. 1824; Baillon, Ann. Sc. Nat. 9: 193. 1858; Boissier, DC. Prodr. 15(2): 188. 1862; Bentham, Gen. Pl. 3: 261. 1880; Hutchinson, Fl. Trop. Afr. 6(1): 607. 1912; Pax & Hoffm., Natürl. Pflanzenfam. ed. 2, 19c: 207. 1931; Keay, Fl. W. Trop. Afr. ed. 2, 1: 416. 1958; Berhaut, Fl. Ill. Sénégal 3: 379. 1975. TYPE: *Anthostema senegalense* A. Juss.

A paleotropical genus of three species, two in west Africa and one in Madagascar.

301. Dichostemma Pierre, Bull. Mens. Soc. Linn. Paris 1 (159): 1259. 1896; Hutchinson, Fl. Trop. Afr. 6(1): 605. 1912; Pax & Hoffm., Natürl. Pflanzenfam. ed. 2, 19c: 207. 1931; Keay, Fl. W. Trop. Afr. ed. 2, 1: 416. 1958. TYPE: *Dichostemma glaucescens* Pierre.

A genus of three species in tropical west Africa.

Subtribe 49b. NEOGUILLAUMINIINAE Croizat, Phil. J. Sci. 64: 408. 1938; Webster, Taxon 24: 601. 1975. TYPE: *Neoguillauminia* Croiz.

Trees or shrubs; indumentum absent; leaves alternate or opposite, entire; stipules obsolete; cyathia in axillary pedunculate cymes; involucral bracts 4(5), dilated or petaloid, connate near base; glands 4, 8, or 10, in 4 or 5 pairs, partitioning the staminate inflorescences; pistillate flower central, staminate flowers in bracteate monochasia; staminate calyx absent; pistillate sepals 5 or 6, imbricate; ovary 3-locular; styles connate at base, unlobed, dilated; fruit capsular; seeds smooth, carunculate.

As defined by Webster (1975), this subtribe includes two Australasian genera. In their pseudopetals developed from the involucral bracts, the cyathia of the Neoguillauminiinae are distinctively different from those in *Euphorbia*, with appendages developed from the interbracteal glands.

KEY TO THE GENERA OF SUBTRIBE NEOGUILLAUMINIIAE

1a. Cyathial glands 8 or 10, massive; petaloid involucral bracts large (ca. 1 cm long); leaves spiral ..... 302. *Neoguillauminia*
1b. Cyathial glands 4, small; involucral bracts, if petaloid, less than 1 cm long; leaves opposite ..... 303. *Calycopeplus*

302. Neoguillauminia Croizat, Phil. J. Sci. 64: 398. 1938; Bull. Jard. Bot. Buit. III. 17: 206. 1941; Guillaumin, Fl. Anal. Synopt. Nouv.-Caléd. 182. 1948; McPherson & Tirel, Fl. Nouv.-Caléd. 14(1): 22, t. 3. 1987. TYPE: *Neoguillauminia cleopatra* (Baill.) Croiz. [*Euphorbia cleopatra* Baill.].

A monotypic New Caledonian genus, very different in habit from its Australian sister genus.

303. Calycopeplus Planchon, Bull. Soc. Bot. France 8: 30. 1861; Boissier, Ic. Euphorb. t. 120. 1866; Bentham, Fl. Austral. 6: 52. 1873; Gen. Pl. 3: 261. 1880; Pax & Hoffm., Natürl. Pflanzenfam. ed. 2, 19c: 221. 1931; Airy Shaw, Kew Bull. 35: 603. 1980. TYPE: *Calycopeplus ephedroides* Planch.

A genus of three species endemic to Australia; although xeromorphic in vegetative morphology, they have cyathia that approach those of the Anthosteminae in structure.

Subtribe 49c. EUPHORBIINAE. TYPE: *Euphorbia* L.

Family Pedilanthaceae Kl. & Gcke., Monatsber. Preuss. Akad. Wiss. Berlin 1859: 247, 253. 1859. Euphorbieae subtribe Pedilanthinae (Kl. & Gcke.) Hurusawa, J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 6: 226. 1954. TYPE: *Pedilanthus* Poit.

Euphorbieae subtribe Anisophyllae Kl. & Gcke., Monatsber. Preuss. Akad. Wiss. Berlin 1859: 247. 1859. TYPE: *Anisophyllum* Haw. [= *Chamaesyce* S. F. Gray].

Euphorbieae subtribe Tithymalinae Kl. & Gcke., Monatsber. Preuss. Akad. Wiss. Berlin 1859: 247. 1859. TYPE: *Tithymalus* Scopoli [= *Euphorbia* L.].

Monoecious (rarely dioecious) trees, shrubs, or herbs; latex milky, innocuous or toxic; indumentum simple or absent; leaves alternate, opposite, or whorled, unlobed (rarely lobed), usually pinnately veined, stipulate or exstipulate; inflorescences terminal or axillary, cyathia often subtended by paired bracts; cyathium distinctly cupulate with 4 or 5 interbracteal glands on the rim (rarely glands only 1 or 2); glands usually discrete, with or without petaloid appendages; pistillate flower central, staminate flowers in 4 or 5 monochasia, monochasial bracts reduced; staminate calyx absent; pistillate calyx 3–6-lobed, or often vestigial or absent; ovary 3-locular; styles distinct or connate, bifid (rarely entire); fruit capsular (rarely drupaceous); seeds carunculate or ecarunculate.

The subtribe is here considered to include seven genera, although some authors have subdivided *Euphorbia* into many segregates. There appears to be no necessity for further subdivision into subtribes such as the Pedilanthinae. Typification of the taxa is reviewed by Wheeler (1943).

KEY TO THE GENERA OF SUBTRIBE EUPHORBIINAE

1a. Cyathia (±) radially symmetrical, the glands not hidden within a nectar spur; styles mostly free or nearly so.
2a. Involucral glands (1–)4 or 5, free, alternating with the lobes of the cyathium along the rim.
3a. Leaves alternate, opposite, or whorled, but if opposite then not inaequilateral at base; veins of leaf not chlorenchyma-sheathed; stipules present or absent; main (embryonic) axis not aborting; seeds carunculate or ecarunculate ..... 304. *Euphorbia*
3b. Leaves opposite, stipulate, inaequilateral at base, veins with chlorenchyma sheaths; main axis ceasing growth above the cotyledons; seeds usually ecarunculate ..... 305. *Chamaesyce*
2b. Involucral glands not 4 or 5 alternating with lobes; bracts subtending cyathium connate into a cup.
4a. Pistillate flower calyculate; involucral lobes fused and the 2 glands fused into a shield; seeds ecarunculate; stems not succulent ..... 306. *Cubanthus*
4b. Pistillate flower naked; involucre and glands connate into an annular ring; seeds mostly carunculate; stems succulent.
5a. Cyathium somewhat bilaterally symmetrical, the gland with a gap on the lower side ..... 307. *Monadenium*
5b. Cyathium radially symmetrical, without a gap on one side.
6a. Involucral glands conspicuous, ovary without angular crests ..... 308. *Synadenium*
6b. Involucral glands distinct, located below the crenulate rim; ovary with prominent double crests at the angles ..... 309. *Endadenium*

1b. Cyathium distinctly bilaterally symmetrical, the glands hidden within the nectar spur; styles connate into a long column ..... 310. *Pedilanthus*

304. Euphorbia L., Sp. Pl. 450. 1753; Gen. Pl. ed. 5, 208. 1754; Roeper, Enum. Euphorb. Germ. 9. 1824; Boissier, DC. Prodr. 15(2): 7. 1862; Icones Euphorbiarum, 1. 1866; Muell. Arg., Fl. Bras. 11(2): 666. 1874; Bentham, Gen. Pl. 3: 258. 1880; Norton, Ann. Rep. Missouri Bot. Gard. 11: 85. 1899; Pax, Bot. Jahrb. 34: 61. 1905; Berger, Sukkulente Euphorbien 1. 1907; N. E. Brown, Fl. Trop. Afr. 6(1): 470. 1911; Fl. Capensis 5(2): 222. 1925; Pax & Hoffm., Natürl. Pflanzenfam. ed. 2, 19c: 208. 1931; Prokhanov, Consp. Syst. Tithymal. Asiae Mediae. 1933; Croizat, Bull. Jard. Bot. Buitenzorg III. 16: 351. 1940; Hurusawa, J. Jap. Bot. 16: 330. 1940; White, A., R. A. Dyer & B. L. Sloane, Succul. Euphorbieae. 1941; Wheeler, Amer. Midl. Nat. 30: 478. 1943; Leandri, Not. Syst. Paris 12: 64. 1946; Vindt, Trav. Inst. Sci. Chérifien 6: 23. 1953; Ursch & Leandri, Mém. Inst. Sci. Madag. 5B: 109. 1954; Dyer, Bull. Jard. Bot. Etat 27: 487. 1957; Dressler, Ann. Missouri Bot. Gard. 48: 329. 1961; Croizat, Webbia 20: 573. 1965; Webster, J. Arnold Arbor. 49: 395. 1967; Radcliffe-Smith & Tutin, Fl. Europaea 2: 213. 1968; Allem & Irgang, Fl. Ilustr. Rio Grande do Sul 11: 15. 1975; M. C. Johnston, Wrightia 5: 120. 1975; Leach, Dinteria 12: 1. 1976; Hassall, Austral. J. Bot. 25: 430. 1977; Subils, Kurtziana 10: 83. 1977; Carter, Hook. Ic. Pl. 39: 5. 1982; Huft, Ann. Missouri Bot. Gard. 71: 1021. 1984; McPherson & Tirel, Fl. Nouv.-Caléd. 14(1): 10. 1987; Gilbert, Kew Bull. 42: 231. 1987; Carter, Kew Bull. 42: 673. 1987; Fl. E. Trop. Afr., Euphorb. 2: 409. 1988; Deil & Müller-Hohenstein, Euphorbia J. 5: 109. 1988; Lebrun & Stork, Enum. Pl. Afr. Trop. 1: 213. 1991; Mayfield, Sida 14: 573. 1991; Lewton, Euphorbia J. 8: 113. 1992. TYPE: *Euphorbia antiquorum* L. (lectotype, designated by Millspaugh, Publ. Field Columbian Mus., Bot. 2: 306. 1909].

Tithymalus Gaertner, Fruct. 2: 115. 1790, nom. cons. TYPE: *Tithymalus peplus* (L.) Gaertner (= *Euphorbia peplus* L.].

Dactylanthes anacantha (Ait.) Haw. [= *Euphorbia anacantha* Ait; lectotype].

Esula (Persoon) Hayworth, Syn. Pl. Succul. 153. 1812 (non Morandi, 1761). TYPE: *Esula dalechampii* Haw. [= *Euphorbia esula* L.].

Galarhoeus Haworth, Syn. Pl. Succul. 143. 1812. TYPE: *Galarhoeus helioscopius* (L.) Haw. [= *Euphorbia helioscopia* L.].

Medusea Haworth, Syn. Pl. Succul. 133. 1812. TYPE: *Medusea major* (Ait.) Haw. [= *Euphorbia caput-medusae* L. var. *major* Ait.; lectotype].

Treisia Haworth, Syn. Pl. Succul. 131. 1812. TYPE: *Treisia clava* (Jacq.) Haw. [= *Euphorbia clava* Jacq.].

Poinsettia Grahm, Edinb. New Phil. J. 20: 412. 1836. TYPE: *Poinsettia pulcherrima* (Willd.) Graham [= *Euphorbia pulcherrima* Willd.].

Lacanthis Rafinesque, Fl. Tell. 2: 94. 1837. TYPE: *Lacanthis splendens* (Boj.) Raf. [= *Euphorbia splendens* Boj. = *E. milii* Desm.].

Agaloma Rafinesque, Fl. Tell. 4: 116. 1838. TYPE: *Euphorbia corollata* L. [lectotype].

Alectoroctonum Schlecht., Linnaea 19: 252. 1847. TYPE: *Alectoroctonum scotanum* Schlecht. [= *Euphorbia scotana* Schlecht.].

Anthacantha Lemaire, Ill. Hort. 4: Misc. 73. 1857. TYPE: *Euphorbia heptagona* L. [lectotype].

Adenopetalum Klotzsch & Garcke, Monatsber. Königl. Preuss. Akad. Wiss. Berlin 1859: 250. 1859 (non Turcz., 1858). TYPE: *Euphorbia graminea* Jacq. [lectotype].

Arthrothamnus Kl. & Gcke., Monatsber. Königl. Preuss Akad. Wiss. Berlin 1859: 251. 1859 (non Ruprecht, 1848). TYPE: *Arthrothamnus tirucalli* (L.) Kl. & Gcke. [= *Euphorbia tirucalli* L.].

Dichrophyllum Klotzsch & Garcke, Monatsber. Königl. Preuss. Akad. Wiss. Berlin 1859: 249. 1859. TYPE: *Dichrophyllum marginatum* (HBK) Kl. & Gcke. [= *Euphorbia marginata* HBK].

Euphorbiastrum Klotzsch & Garcke, Monatsber. Königl Preuss. Akad. Wiss. Berlin 1859: 252. 1859. TYPE: *Euphorbiastrum hoffmannianum* Kl. & Gcke. [= *Euphorbia hoffmanniana* (Kl. & Gcke.) Boiss.; lectotype].

Sterigmanthe Klotzsch & Garcke, Monatsber. Königl Preuss. Akad. Wiss. Berlin 1859: 252. 1859. TYPE: *Euphorbia splendens* Boj. [= *Euphorbia milii* Desm.; lectotype].

Tithymalopsis Klotzsch & Garcke, Monatsber. Königl Preuss. Akad. Wiss. Berlin 1859: 249. 1859. TYPE: *Euphorbia corollata* L. [lectotype].

Trichosterigma Klotzsch & Garcke, Monatsber. Königl Preuss. Akad. Wiss. Berlin 1859: 248. 1859. TYPE: *Euphorbia fulgens* Karw. [lectotype].

Lyciopsis (Boissier) Schweinfurth, Beitr. Fl. Aethiop. 37. 1867 (non Spach, 1835). TYPE: *Euphorbia carneata* Vahl.

Elaeophorbia Stapf, in Johnston, Liberia 2: 646. 1906. TYPE: *Elaeophorbia drupacea* (Schum.) Stapf [= *Euphorbia drupacea* Schum.].

Diplocyathium H. Schmidt, Beih. Bot. Centralbl. 22(1) 40. 1907. TYPE: *Diplocyathium capitulatum* (Rchb.) Schmidt [= *Euphorbia capitulata* Rchb.].

Euphorbiodendron Millspaugh, Publ. Field Columbian Mus. Bot. 2: 305. 1909. TYPE: *Euphorbiodendron latazii* (HBK) Millsp. [= *Euphorbia latazii* HBK lectotype, chosen here; perhaps = *Euphorbia laurifolia* Lam.].

Ctenadena Prokhanov, Consp. Syst. Tithymal. Asiae Me

diae 28. 1933. TYPE: *Ctenadena lanata* (Sieb.) Prokh. [= *Euphorbia lanata* Sieb.].

Cystidospermum Prokhanov, Consp. Syst. Tithymal. Asiae Mediae 25. 1933. TYPE: *Cystidospermum cheirolepis* (Fisch. & Mey.) Prokh. [= *Euphorbia cheirolepis* Fisch. & Mey.].

Sclerocyathium Prokhanov, Consp. Syst. Tithymal. Asiae Mediae 30. 1933. TYPE: *Sclerocyathium popovii* Prokh. [= *Euphorbia sclerocyathium* Korov. & Pop.].

A vast genus of over 1000 species, subdivided into many subgenera and sections, a number of which have been treated as distinct genera. The large number of synonyms cited here (lectotypifications by Wheeler, 1943) represents only a fraction of the published names that are referable to *Euphorbia*; they have been chosen because in the literature they have been treated as distinct at the generic or subgeneric level. The literature on *Euphorbia*, especially the succulent taxa, is vast, and it is not possible to cite here even a fraction of the relevant papers, including many important papers on succulent taxa by Leach and Rauh. Many references are provided by Wheeler (1943), Vindt (1960), Webster (1967), Carter & Radcliffe-Smith (1988), and Lebrun & Stork (1991); and numbers of taxa are discussed and illustrated in the eight volumes of the *Euphorbia Journal*. Nevertheless, there is great need for a comprehensive bibliographic guide to the taxonomic work on *Euphorbia* that would complement the list of species of Oudejans (1990). Some segregates, especially *Poinsettia*, have been adopted by a number of workers, and it remains to be seen if future work will confirm the conservative generic circumscription adopted by Boissier and his followers.

305. Chamaesyce S. F. Gray, Nat. Arrang. Brit. Pl. 2: 260. 1821; Croizat & Degener, Fl. Haw. 1936; Wheeler, Rhodora 43: 97. 1941; Burch, Ann. Missouri Bot. Gard. 53: 90. 1966; Webster, J. Arnold Arbor. 48: 420. 1967; Hassall, Austral. J. Bot. 24: 633. 1976; Mulligan & Lindsay, Naturaliste Canad. 105: 37–40. 1978; Koutnik, S. Afr. J. Bot. 3: 262. 1984; Allertonia 4(6): 331. 1987. TYPE: *Chamaesyce maritima* S. F. Gray [= *Chamaesyce peplis* (L.) Prokh.].

Anisophyllum Haworth, Syn. Pl. Succ. 159. 1812 (non Jacquin, 1763). TYPE: *Anisophyllum peplis* (L.) Haw. [= *Chamaesyce peplis* (L.) Prokh.].

A widely distributed genus of ca. 250 species, most of them in tropical America and Africa; often treated as a subgenus of *Euphorbia*. Koutnik (1987) presented the most detailed analysis of the characters that support generic status for *Chamaesyce*. However, it must be admitted that *Euphorbia* subsect. *Acutae* is in many ways intermediate between *Chamaesyce* and *Euphorbia* subg. *Agaloma*. By strictly phylogenetic criteria, conservative workers are correct in retaining *Chamaesyce* as a subgenus of *Euphorbia*, because its recognition makes the latter a paraphyletic group. An obvious solution to this is to further dismantle *Euphorbia* into segregate genera, in the tradition of Klotzsch and Garcke. However, this would not get workers using cladistic methodology off the hook, because a monophyletic *Chamaesyce* would probably have to include both *Euphorbia* subg. *Agaloma* as well as *Pedilanthus* and possibly *Cubanthus*. Until a detailed phylogenetic analysis of the Euphorbieae is completed, we have no practical alternative to continuing the use of the present artificial (but reasonably usable) system.

306. Cubanthus (Boissier) Millspaugh, Field Mus. Nat. Hist. Bot. 2: 371. 1913; Alain, Fl. Cuba 3: 127. 1953. TYPE: *Cubanthus linearifolius* (Griseb.) Millsp. [*Pedilanthus linearifolius* Griseb.].

A genus of three species endemic to the West Indies (Cuba and Hispaniola); very similar to species of *Euphorbia* sect. *Adenorima*, and perhaps to be included in that group.

307. Monadenium Pax, Bot. Jahrb. 19: 126. 1894; N. E. Brown, Fl. Trop. Afr. 6(1): 450. 1911; Pax & Hoffm., Natürl. Pflanzenfam. ed. 2, 19c: 222. 1931; Bally, Genus *Monadenium*, 14. 1961; Carter, Kew Bull. 42: 903. 1987; Fl. E. Trop. Afr., Euphorb. 2: 540. 1988. TYPE: *Monadenium coccineum* Pax.

Stenadenium Pax, Bot. Jahrb. 30: 343. 1901. TYPE: *Stenadenium spinescens* Pax [= *Monadenium spinescens* (Pax) Bally].

An African genus of ca. 50 species, distributed from Somalia to the Transvaal.

308. Synadenium Boissier, DC. Prodr. 15(2): 187. 187. 1862; N. E. Brown, Fl. Trop. Afr. 6(1): 462. 1911; Pax & Hoffm., Natürl. Pflanzenfam. ed. 2, 19c: 221. 1931; White, Dyer, & Sloane, Succ. Euphorbieae 951. 1941; Carter, Kew Bull. 42: 667. 1987; Fl. E. Trop. Afr., Euphorb. 2: 534. 1988. TYPE: *Synadenium arborescens* Boissier [= *Synadenium cupulare* (Boiss.) L. C. Wheeler].

A genus of 10–15 species of eastern and southern Africa, closely related to *Monadenium*.

309. Endadenium Leach, Garcia de Orta 1: 31. 1973. TYPE: *Endadenium gossweileri* (N. E. Brown) Leach.

A monotypic genus of Angola; perhaps not distinct from the genus *Monadenium*.

310. Pedilanthus Necker ex Poiteau, Ann. Mus. Nat. Hist. Nat. 19: 388. 1812; Boissier, DC. Prodr. 15(2): 4. 1862; Millspaugh, Field Mus. Publ. Bot. 2: 353. 1913; Pax & Hoffm., Natürl. Pflanzenfam. ed. 2, 19c: 223. 1931; Wheeler, Contr. Gray Herb. 124: 43. 1939; Dressler, Contr. Gray Herb. 182: 1. 1957; Webster, J. Arnold Arbor. 48: 427. 1967; Koutnik, Euphorbia J. 3: 38. 1985. TYPE: *Pedilanthus tithymaloides* (L.) Poit.

Tithymalus Miller, Gard. Dict. Abr. Ed. 4. 1754. *Tithymaloides* Gomez Ortega, Tabl. Bot. 9. 1773 (nom. rej.). *Crepidaria* Haworth, Syn. Pl. Succ. 136. 1812. TYPE: *Tithymalus myrtifolius* Miller [= *Pedilanthus tithymaloides* (L.) Poit.].

Ventenatia Trattinick, Gen. Pl. 86. 1802 (non Cavanilles, 1798). TYPE: *Ventenatia bracteata* (Jacq.) Trat. [= *Pedilanthus bracteatus* (Jacq.) Boiss.].

Diadenaria Klotzsch & Garcke, Monatsber. Königl. Preuss. Akad. Wiss. Berlin 1859: 254. 1859. TYPE: *Diadenaria pavonis* Kl. & Gcke. [= *Pedilanthus bracteatus* (Jacq.) Boiss.].

Hexadenia Klotzsch & Garcke, Monatsber. Königl. Preuss. Akad. Wiss. Berlin 1859: 253. 1859. TYPE: *Hexadenia macrocarpa* (Benth.) Kl. & Gcke. [= *Pedilanthus macrocarpus* Benth.].

A neotropical genus of ca. 15 species, all except one confined to Mexico and adjacent Central America.

INCERTAE SEDIS

311. Chlamydojatropha Pax & Hoffmann, Pflanzenr. 147. VI (Heft 57): 125. 1912; Natürl. Pflanzenfam., ed. 2, 19c: 167. 1931. TYPE: *Chlamydojatropha kamerunica* Pax & Hoffm.

This mysterious plant, known only from pistillate specimens from Cameroon, was placed next to *Mildbraedia* by Pax & Hoffmann (1931). Until the staminate flowers are described, it cannot be definitely placed.

312. Martretia Beille, Compt. Rend. Hebd. Séances Acad. Sci. (Paris) 145: 1294. 1907; Bull. Soc. Bot. France 55 (Mém. 2) 8: 64. 1908; Pax & Hoffmann, Natürl. Pflanzenfam. ed. 2, 19c: 52. 1931; Léonard, Bull. Jard. Bot. Nat. Belg. 59: 319. 1989. TYPE: *Martretia quadricornis* Beille.

This west African genus of two species was placed next to *Aporusa* by Pax & Hoffmann (1931), but J. Léonard (1989) proposed that it be placed in a new tribe Martretieae Köhler ex Léonard, within subfamily Phyllanthoideae. Meeuse (1990) regarded *Martretia* as more appropriately included in the Acalyphoideae (Chrozophoreae).

313. Tacarcuna Huft, Ann. Missouri Bot. Gard. 76: 1080. 1989. TYPE: *Tacarcuna gentryi* Huft.

This recently described genus of three species from Panama and South America was proposed by the author without any indication of affinity, although the description of uniovulate locules of the ovary, together with the general aspect, would suggest subfamily Acalyphoideae. However, examination of material of an isotype of the type species (*Gentry 16869*, DAV) shows that the ovary has biovulate locules. Although floral structure suggests that *Tacarcuna* belongs to subfamily Phyllanthoideae, and perhaps to tribe Wielandieae (where it may be close to *Savia*), scanning micrographs of pollen (courtesy of Joan Nowicke; Webster, ined.) show a striate exine suggestive of pollen in other tribes such as Antidesmeae or Briedelieae.

314. Avellanita R. A. Philippi, Linnaea 33: 27. 1864. TYPE: *Avellanita bustillosii* R. A. Philippi.

The systematic position of this genus has remained questionable up to the present. In his original description, Philippi assigned *Avellanita* to the "Crotoneae," and Bentham (1880), on the basis of that desciption alone, placed it in tribe Crotoneae between *Micrandra* and *Hevea*. Pax (1910), following these earlier dispositions, located *Avellanita* within tribe Jatropheae following *Garcia*; however, he noted that its habit was aberrant and its leaves suggestive of *Argythamnia*. Pax & Hoffmann (1931), in an abrupt shift of opinion, assigned *Avellanita* to tribe Acalypheae, in juxtaposition with the Old World genera *Trewia* and *Melanolepis*. Croizat, in manuscript notes (1960) on a specimen in the Chilean Museo Nacional de Historia Natural (SGO), remarked on the vegetative similarity of *Avellanita* to genera of Chrozophoreae; however, the apetalous flowers and polyandrous androecium of the Chilean plant would be quite discordant with that tribe.

Examination of scanning micrographs from a specimen in the Museo Nacional (SGO 051523) clearly contradicts an assignment of *Avellanita* to subfamily Crotonoideae, as the exine does not show a Croton-pattern. The 3-colporate grains with rather coarse muri topped by nanospinules are somewhat similar to those in tribe Adelieae subfam. Acalyphoideae, but they are also not dissimilar to the grains found in tribe Acalypheae, e.g., *Trewia*. Although the precise affinity of *Avellanita* remains ambiguous, the evidence from pollen and floral characters clearly points to its placement within subfamily Acalyphoideae.

315. Cubacroton Alain, Candollea 17: 116. 1960. TYPE: *Cubacroton maestrense* Alain.

I have not been able to examine material of this enigmatic genus, which is known only from the type collection in the Sierra de Maestra, Cuba. Judging from the description, the plant probably belongs in tribe Crotoneae; it appears similar to the Cuban endemic genus *Moacroton*, and possibly may prove to be an aberrant species of that genus.

ADDENDUM

316. Dendrothrix Esser, Novon 3: 245. 1993. TYPE: *Dendrothrix yutajensis* (Jabl.) Esser.

This genus, referred by its author to subtribe Mabeinae, was published too late to be accommodated in the main sequence of this synopsis. It is related to *Senefelderopsis*, and therefore should be inserted in subtribe Mabeinae following that genus. Esser provides several keys to distinguish *Dendrothrix* from the other genera of Mabeinae.

317. Cladogelonium Leandri, Bull. Soc. Bot. France 85: 530. 1939. TYPE: *Cladogelonium madagascariense* Leandri.

This monotypic genus from Madagascar remains poorly known. Judging from the description and illustration, it does appear to be similar to the widespread paleotropical genus *Suregada*, so it may prove to belong to tribe Gelonieae.

EXCLUDED TAXA

1. **Burseranthe** Rizzini, Leandra 4/5: 5. 1974. TYPE: ***Burseranthe pinnata*** Rizz.

This monotypic genus, based on a single species from eastern Brazil (Alagoas), was referred to subfamily Phyllanthoideae by Rizzini. The plant, however, has pinnate leaves, which are otherwise unknown in the family (except for the dubious case of *Bischofia*). Examination of authentic material (kindly furnished by Rizzini) shows that the plant belongs to the Meliaceae and, following the treatment of Pennington (1981), clearly represents *Trichilia lepidota* Mart. subsp. *lepidota*.

2. **Casabitoa** Alain, Phytologia 47: 175. 1980; Fl. Española 4: 92. 1986. TYPE: *Casabitoa perfae* Alain.

This inadequately characterized genus, based on pistillate specimens of a single species from Hispaniola, is not euphorbiaceous. According to Tom Zanoni (in press), who visited the type locality, the plant is a species of Simarubaceae (*Picramnia dictyoneura* (Urb.) Urb.).

3. **Polygonanthus** Ducke, Notizbl. Bot. Gart. Berlin 11: 345. 1932. TYPE: *Polygonanthus amazonicus* Ducke.

The genus is not euphorbiaceous, although its systematic position has been controversial. Although Baehni & Dansereau (1939) referred *Polygonanthus* to the Saxifragaceae (sensu lato), placement in the Anisophylleaceae by Pires and Rodrigues (1971) probably has the most support (e.g., in Cronquist, 1981).

4. **Pseudocroton** Muell. Arg., Flora 55: 24. 1872; Huft, Ann. Missouri Bot. Gard. 69: 429. 1982. TYPE: *Pseudocroton tinctorius* [= *Capparis indica* (L.) Fawc. & Rend.].

5. **Skutchia** Pax & Hoffmann, J. Wash. Acad. Sci. 27: 306. 1937; Burger, Fieldiana Bot. 40: 212. 1977. TYPE: *Skutchia caudata* Pax & Hoffm. [= *Trophis mexicana* (Liebm.) Bur.].

6. **Trisyngyne** Baillon, Adansonia 11: 136. 1874; Bauman-Bodenheim, Bull. Mus. Hist. Nat. Paris II. 25: 420. 1953; Steenis, Adansonia II. 11: 615. 1971. TYPE: not designated (Baillon published 2 species: *Trisyngyne balansae* and *T. codonandra*; but neither Bauman-Bodenheim nor van Steenis designated a type).

The New Caledonian genus *Trisyngyne* was reduced by van Steenis (1971) to *Nothofagus* subsect. *Bipartitae*.

LITERATURE CITED

AIRY SHAW, H. K. 1961. Notes on Malaysian Euphorbiaceae. Kew Bull. 14: 353–397.

———. 1963. A synopsis of the genus *Ptychopyxis* Miq. Kew Bull. 14: 363–374.
———. 1965. Diagnoses of new families, new names, etc. for the seventh edition of Willis's "Dictionary." Kew Bull. 18: 249–272.
———. 1966. Willis' Dictionary of the Flowering Plants and Ferns, Addenda [pp. xxi, xxii]. Cambridge Univ. Press, Cambridge.
———. 1967. Notes on Malaysian and other Asiatic Euphorbiaceae. Kew Bull. 20: 379–414.
———. "1971" [1972]. The Euphorbiaceae of Siam. Kew Bull. 26: 191–363.
———. 1974. Noteworthy Euphorbiaceae from tropical Asia (Burma to New Guinea). Hook. Ic. Pl. 38(1): 3701–3725.
———. 1975. The Euphorbiaceae of Borneo. Kew Bull. Add. Ser. 4: 1–245.
———. 1980. A partial synopsis of the Euphorbiaceae — Platylobeae of Australia (excluding *Phyllanthus*, *Euphorbia*, and *Calycopeplus*). Kew Bull. 35: 577–700.
———. 1981. The Euphorbiaceae of Sumatra. Kew Bull. 36: 239–374.
Baehni, C. & P. Dansereau. 1939. *Polygonanthus*, genre de Saxifragacées. Bull. Soc. Bot. France 86: 183–186.
Baillon, H. 1858. Etude Générale du Groupe des Euphorbiacées. Victor Masson, Paris.
———. 1865. Remarques générales sur les Stillingiidées du Brésil. Adansonia, I. 5: 336–344.
———. 1866. Sur deux Euphorbiacées brésiliennes. Adansonia, I. 6: 231–237.
Baldwin, J. & R. Schultes. 1947. A conspectus of the genus *Cunuria*. Bot. Mus. Leafl. Harvard Univ. 12: 325–351.
Bentham, G. 1878. Notes on Euphorbiaceae. J. Linn. Soc. London, Bot. 17: 185–267.
———. 1880. Euphorbiaceae. *In*: G. Bentham & J. D. Hooker, Genera Plantarum 3: 239–340.
Bhatnagar, A. K. & R. N. Kapil. 1974. *Bischofia javanica* – Its relationship with Euphorbiaceae. Phytomorphology 23: 264–267.
Borhidi, A. 1972. La taxonomia del género *Platygyne* Merc. Ann. Hist. Nat. Mus. Hung. 64: 89–94.
Carter, S. & A. Radcliffe-Smith. 1988. Euphorbiaceae Part 2. Fl. Trop. E. Africa. 409–597.
Chapman, A. D. 1991. Australian Plant Name Index. Australian Government Publishing Service, Canberra.
Croizat, L. 1941a. The Tribe Plukenetiinae of the Euphorbiaceae in eastern tropical Asia. J. Arnold Arbor. 22: 417–431.
———. 1941b. Notes on the Euphorbiaceae II. 1. The systematic position of the *Omphalea*. Bull. Jard. Bot. Buitenzorg. ser. 3, 17: 204–208.
———. 1942. On certain Euphorbiaceae from the tropical Far East. J. Arnold Arbor. 23: 29–54.
Cronquist, A. 1981. An Integrated System of Classification of Flowering Plants. Columbia Univ. Press, New York.
Dehgan, B. & G. L. Webster. 1979. Morphology and infrageneric relationships of the genus *Jatropha* (Euphorbiaceae). Univ. California Publ. Bot. 74: 1–73.
Dressler, R. L. 1954. The genus *Tetracoccus* (Euphorbiaceae). Rhodora 56: 45–61.
Ducke, A. 1925. Plantes nouvelles ou peu connues de la région amazonienne. III. Arq. Jard. Bot. Rio Janeiro 4: 1–208.
Erdtman, G. 1952. Pollen Morphology and Plant Taxonomy. Almqvist & Wiksells, Uppsala.
Farr, E. R., J. A. Leussink & F. A. Stafleu (editors). 1979. Index Nominum Genericorum (Plantarum). 3 vols. Bohn, Scheltema & Holkema, Utrecht.
Forman, L. L. 1966. The reinstatement of *Galearia* Zoll. et Mor. and *Microdesmis* Hook. f. in the Pandaceae. Kew Bull. 20: 309–321.
———. 1971. A synopsis of *Galearia* Zoll. and Mor. (Pandaceae). Kew Bull. 26: 153–165.
Gagnepain, F. & L. Beille. 1926. Euphorbiacées. Fl. Generale Indo-Chine 5: 373–516.
Gehrmann. 1908. Vorarbeiten zu einer Monographie der Gattung *Bridelia* mit besonderer Berücksichtigung der afrikanischen Arten. Bot. Jahrb. 41(Beibl. 95): 1–42.
Gilg, E. 1908. Flacourtiaceae Africanae. *In*: A. Engler (editor), Beiträge zur Flora von Afriken 32. Bot. Jahrb. 40: 444–518.
Gillespie, L. 1993. A synopsis of neotropical *Plukenetia* (Euphorbiaceae) including two new species. Syst. Bot. 18: 575–592.
Grüning, G. 1913. Euphorbiaceae–Porantheroideae & Ricinicarpoideae. *In*: A. Engler (editor), Das Pflanzenreich IV. 147 (Heft 58): 1–97.
Hans, A. S. 1973. Chromosomal conspectus of the Euphorbiaceae. Taxon 22: 591–636.
Henderson, R. J. F. 1993. Studies in Euphorbiaceae A. L. Juss., sens. lat. 1. A revision of *Amperea* Adr. Juss. (Acalyphoideae Ascherson, Ampereae Muell. Arg.). Austral. Syst. Bot. 10 (in press).
Hooker, J. D. 1887. Flora of British India, Vol. 5. L. Reeve, London.
Huft, M. 1989. New and critical taxa of Euphorbiaceae from South America. Ann. Missouri Bot. Gard. 76: 1077–1086.
Hurusawa, I. 1954. Eine nochmalige Durchsicht des herkömmlichen Systems der Euphorbiaceen im weiteren Sinne. J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 6: 209–342.
Hutchinson, J. 1911–1912. Euphorbiaceae [in part]. *In*: W. T. Thistleton-Dyer (editor), Flora of Tropical Africa, Vol. 6; section 1: 441–1059.
Hutchinson, J. 1969. Tribalism in the family Euphorbiaceae. Amer. J. Bot. 56: 738–758.
Ingram, J. 1967. A revisional study of *Argythamnia* subgenus *Argythamnia* (Euphorbiaceae). Gentes Herb. 10: 1–38.
———. 1979. The generic limits of *Argythamnia* (Euphorbiaceae) defined. Gentes Herb. 11: 426–436.
Jablonski, E. 1967. Euphorbiaceae. *In*: B. Maguire (editor), Botany of Guayana Highland – Part VII. Mem. New York Bot. Gard. 17: 80–190.
Jussieu, A. 1824. De Euphorbiacearum generibus medicisque earumdem tentamen. Didot, Paris.
Köhler, E. 1965. Die Pollenmorphologie der biovulaten Euphorbiaceae und ihre Bedeutung für die Taxonomie. Grana Palynol. 6: 26–120.
Koutnik, D. L. 1987. A taxonomic revision of the Hawaiian species of the genus *Chamaesyce* (Euphorbiaceae). Allertonia 4: 331–388.
Kruijt, R. C. & G. Zijlstra. 1989. Proposal to conserve 4483 *Sapium* Jacq., 1760 against P. Browne, 1756 (Euphorbiaceae). Taxon 38: 320–325.

Leandri, J. 1958. Euphorbiacées. Fl. Madagascar 111: 1–209.

Lebrun, J.-P. & A. L. Stork. 1991. Enumération des Plantes à Fleurs d'Afrique Tropicale, Vol. I. Généralités et Annonaceae à Pandaceae. Conservatoire et Jardin Botaniques de la Ville de Genève, Geneva.

Léonard, J. 1951. Espèces congolaises nouvelles ou intéressantes. Bull. Soc. Roy. Bot. Belg. 84: 47–60.

———. 1956. Notulae Systematicae 21. Observations sur les genres *Oldfieldia*, *Paivaeusa* et *Cecchia* (Euphorbiaceae africanae). Bull. Jard. Bot. Brux. 26: 335–343.

———. 1959. Observations sur les genres *Pycnocoma* et *Argomuellera* (Euphorbiacées africanes). Bull. Soc. Roy. Bot. Belg. 91: 267–281.

———. 1962a. Euphorbiaceae. Fl. Congo 8(1): 1–214.

———. 1962b. Notulae Systematicae 33. Sur les limites entre les genres *Drypetes* Vahl et *Lingelsheimia* Pax (Euphorbiaceae). Bull. Jard. Bot. Brux. 32: 513–516.

———. 1989. Revision du genre africain *Martretia* Beille (Euphorbiaceae) et la nouvelle tribu des Martretieae. Bull. Jard. Bot. Nat. Belg. 59: 319–332.

——— & M. Mosango. 1985. Hymenocardiaceae. Flore d'Afrique Centrale: Spermatophytes. Jardin Botanique National de Belgique, Bruxelles.

Levin, G. A. 1986a. Systematic foliar morphology of Phyllanthoideae (Euphorbiaceae), I. Conspectus. Ann. Missouri Bot. Gard. 73: 29–85.

———. 1986b. Systematic foliar morphology of Phyllanthoideae (Euphorbiaceae). II. Phenetic analysis. Ann. Missouri Bot. Gard. 73: 86–98.

———. 1986c. Systematic foliar morphology of Phyllanthoideae III. Cladistic analysis. Syst. Bot. 11: 515–530.

——— & M. G. Simpson. 1994. Phylogenetic implications of pollen ultrastructure in the Oldfieldioideae (Euphorbiaceae). Ann. Missouri Bot. Gard. 81: 203–238.

Lindley, J. 1836. A Natural System of Botany, 2nd ed. Longman, Rees, Orme, Brown, Green, and Longman, London.

Liogier, A. H. 1971. Novitates antillanae. Mem. New York Bot. Gard. 21: 107–157.

McPherson, G. & C. Tirel. 1987. Euphorbiacées. Fl. Nouv.-Caléd. 14(1): 1–226.

McVaugh, R. 1944. The genus *Cnidoscolus*: Generic limits and intrageneric groups. Bull. Torrey Bot. Club 71: 457–474.

Meeuse, A. D. J. 1990. The Euphorbiaceae auct. plur.: An Unnatural Taxon. Eburon, Delft.

Mennega, A. M. W. 1987. Wood anatomy of the Euphorbiaceae, in particular of the subfamily Phyllanthoideae. Bot. J. Linn. Soc. 94: 111–126.

Merrill, E. D. 1935. A commentary on Loureiro's "Flora Cochinchinensis." Trans. Amer. Philos. Soc. 24: 1–49.

Miller, K. & G. L. Webster. 1962. Systematic position of *Cnidoscolus* and *Jatropha*. Brittonia 14: 174–180.

Mueller, J. 1865. Euphorbiaceae. Linnaea 34: 1–224.

———. 1866. Euphorbiaceae. *In*: DC., Prodromus 15(2): 189–1261.

———. 1874. Euphorbiaceae [part 2]. *In*: Martius, Fl. Brasiliensis 11(2): 293–750.

Oudejans, R. C. H. M. 1990. World Catalogue of Species Names Published in the Tribe Euphorbieae (Euphorbiaceae) with Their Geographical Distribution. Oudejans, Utrecht [self-published].

Pax, F. 1890. Euphorbiaceae. *In*: A. Engler & K. Prantl, Die Natürlichen Pflanzenfamilien, ed. 1, 3(5): 1–119.

———. 1910. Euphorbiaceae–Jatropheae. *In*: A. Engler (editor), Das Pflanzenreich IV. 147. [I] (Heft 42): 1–148.

———. 1924. Die Phylogenie der Euphorbiaceae. Bot. Jahrb. 59: 129–182.

——— & K. Hoffmann. 1911. Euphorbiaceae Cluytieae. *In*: A. Engler (editor), Das Pflanzenreich IV. 147. III (Heft 47): 1–124.

——— & ———. 1912. Euphorbiaceae–Gelonieae, Hippomaneae. *In:* A. Engler (editor), Das Pflanzenreich IV. 147. V. (Heft 52): 1–41, 1–319.

——— & ———. 1914. Euphorbiaceae–Acalypheae–Mercurialinae. *In*: A. Engler (editor), Das Pflanzenreich IV. 147. VII (Heft 63): 1–473.

——— & ———. 1919. Euphorbiaceae–Plukenetiinae. *In*: A. Engler (editor), Das Pflanzenreich IV. 147. IX. (Heft 68): 1–108.

——— & ———. 1922. Euphorbiaceae–Phyllantheae. *In*: A. Engler (editor), Das Pflanzenreich IV. 147. XV. (Heft 81): 1–349.

——— & ———. 1931. Euphorbiaceae. *In*: A. Engler & K. Prantl (editors), Die Natürlichen Pflanzenfamilien ed. 2, 19c: 11–233.

Pennington, T. D. 1981. A monograph of neotropical Meliaceae. Fl. Neotrop. 28: 1–470.

Pfeiffer, L. 1874. Nomenclator Botanicus. T. Fischer, Cassell.

Pires, J. M. & W. A. Rodrigues. 1971. Notas sôbre os gêneros *Polygonanthus* e *Anisophyllea*. Acta Amazonica 1(2): 7–15.

Prain, D. 1920. Euphorbiaceae [in part]. *In*: W. T. Thiselton-Dyer (editor), Flora Capensis, Vol. 5, sect. 2: 410–516.

Punt, W. 1962. Pollen morphology of the Euphorbiaceae with special reference to taxonomy. Wentia 7: 1–116.

Radcliffe-Smith, A. 1973. An account of the genus *Cephalocroton* Hochst. (Euphorbiaceae). Kew Bull. 28: 123–132.

———. 1987a. Euphorbiaceae, Part 1. Fl. Trop. E. Afr. 1–407.

———. 1987b. Segregate families from the Euphorbiaceae. Bot. J. Linn. Soc. 94: 47–66.

———. 1988. Notes on Madagascan Euphorbiaceae I. On the identity of *Paragelonium* and the affinities of *Benoistia* and *Claoxylopsis* (Euphorbiaceae). Kew Bull. 43: 625–647.

Rogers, D. J. & S. G. Appan. 1973. *Manihot*, *Manihotoides* (Euphorbiaceae). Fl. Neotrop. 13: 1–272.

Rothmaler, W. 1944. Nomina generica neglecta 1753–1763. Repert. Sp. Nov. 53: 1–37.

Schultes, R. 1952. Studies in the genus *Micrandra* I: The relationship of the genus *Cunuria* to *Micrandra*. Bot. Mus. Leafl. Harvard Univ. 15: 201–222.

———. 1970. The history of taxonomic studies in *Hevea*. Bot. Rev. 36: 197–276.

———. 1990. A brief taxonomic view of the genus

Hevea. Malaysian Rubber Research & Development Board Monograph 14: 1–57.

SECCO, R. 1985. Notas sobre o novo conceito de *Sagotia racemosa* em relação ás suas variedades. Acta Amazonica 15(1–2, suppl.): 81–85.

———. 1988. Dialissepalia do gênero *Sandwithia* Lanj. (Euphorbiaceae): Uma novidade botânica do alto Rio Negro e da Venezuela. Bol. Mus. Par. Emilio Goeldi Bot. 4: 177–185.

———. 1990. Revisão dos gêneros *Anomalocalyx* Ducke, *Dodecastigma* Ducke, *Pausandra* Radlk., *Pogonophora* Miers ex Benth. e *Sagotia* Baill. (Euphorbiaceae–Crotonoideae) para a América do Sul. Museu Paraense Emilio Goeldi, Belem.

——— & G. L. WEBSTER. 1990. Materiais para a flora amazonica IX. Ensaio sobre a sistemática de gênero *Richeria*. Bol. Mus. Para. Emilio Goeldi, Bot. 6: 141–158.

STEENIS, C. G. G. J. VAN. 1971. Revision of *Nothofagus* in New Caledonia. Adansonia II. 11: 615 624.

TAKHTAJAN, A. L. 1980. Outline of the classification of flowering plants (Magnoliophyta). Bot. Rev. 46: 225–359.

THIN, N. N. 1984. Tribus Alchornieae (Euphorbiaceae) of Vietnamese Flora. Tap Chi Sinh Hoc 6(3): 26–29.

———. 1988. Tribe Epiprineae (Muell. Arg.) Hurusawa (Euphorbiaceae) in Vietnam. Tap Chi Sinh Hoc 10(2): 30 33.

———. 1989. Tribus Codiaeae (Pax) Hutch. in Vietnam. Tap Chi Sinh Hoc 11(3): 14–17.

THOMAS, D. W. 1990. *Conceveiba* Aublet (Euphorbiaceae) new to Africa. Ann. Missouri Bot. Gard. 77: 856–858.

VINDT, J. 1960. Monographie des Euphorbiacées du Maroc. Index Bibliographique. Trav. Inst. Sci. Chérif., Bot. 19: 482–521.

WEBSTER, G. L. 1956. A monographic study of the West Indian species of *Phyllanthus*. J. Arnold Arbor. 37: 91–122, 217–268, 340–359.

———. 1957. A monographic study of the West Indian species of *Phyllanthus*. J. Arnold Arbor. 38: 51–80, 170–198, 295–373.

———. 1958. A monographic study of the West Indian species of *Phyllanthus*. J. Arnold Arbor. 39: 49–100, 111–212.

———. 1967. The genera of Euphorbiaceae in the southeastern United States. J. Arnold Arbor. 48: 303–430.

———. 1975. Conspectus of a new classification of the Euphorbiaceae. Taxon 24: 593–601.

———. 1983. A botanical gordian knot: The case of *Ateramnus* and *Gymnanthes* (Euphorbiaceae). Taxon 32: 304–305.

———. 1987. The saga of the spurges: A review of classification and relationships in the Euphorbiales. Bot. J. Linn. Soc. 94: 3–46.

———. 1992. Realignments in American *Croton* (Euphorbiaceae). Novon 2: 269–273.

———. 1993. A provisional synopsis of the sections of the genus *Croton* (Euphorbiaceae). Taxon 42: 793–823.

——— & W. S. ARMBRUSTER. 1991. A synopsis of the neotropical species of *Dalechampia* (Euphorbiaceae). Bot. J. Linn. Soc. 105: 137–177.

——— & M. J. HUFT. 1988. Revised synopsis of Panamanian Euphorbiaceae. Ann. Missouri Bot. Gard. 75: 1087–1144.

WHEELER, L. C. 1943. The genera of living Euphorbieae. Amer. Midl. Naturalist 30: 456–503.

———. 1975. Euphorbiaceous genera lectotypified. Taxon 24: 534–538.

APPENDIX 1. Outline of taxa as treated in the text.

I. Subfamily PHYLLANTHOIDEAE
  1. Tribe WIELANDIEAE
    1. Heywoodia
    2. Savia
    3. Gonatogyne
    4. Petalodiscus
    5. Blotia
    6. Actephila
    7. Discocarpus
    8. Lachnostylis
    9. Chonocentrum
    10. Wielandia
  2. Tribe AMANOEAE
    11. Pentabrachion
    12. Amanoa
  3. Tribe BRIEDELIEAE
    13. Cleistanthus
    14. Briedelia
  4. Tribe PHYLLANTHEAE
    4a. Subtribe ASTROCASIINAE
      15. Astrocasia
    4b. Subtribe LEPTOPINAE
      16. Leptopus
    4c. Subtribe PSEUDOLACHNOSTYLIDINAE
      17. Chascotheca
      18. Zimmermannia
      19. Zimmermanniopsis
      20. Meineckia
      21. Pseudolachnostylis
      22. Keayodendron
    4d. Subtribe SECURINEGINAE
      23. Securinega
    4e. Subtribe ANDRACHNINAE
      24. Andrachne
    4f. Subtribe FLUEGGEINAE
      25. Flueggea
      26. Richeriella
      27. Aerisilvaea
      28. Margaritaria
      29. Phyllanthus
      30. Reverchonia
      31. Sauropus
      32. Breynia
      33. Glochidion
  5. Tribe DRYPETEAE
    34. Lingelsheimia
    35. Drypetes
    36. Sibangea
    37. Putranjiva
  6. Tribe ANTIDESMEAE
    6a. Subtribe SPONDIANTHINAE
      38. Spondianthus
    6b. Subtribe UAPACINAE
      39. Uapaca
    6c. Subtribe SCEPINAE
      40. Protomegabaria
      41. Maesobotrya
      42. Richeria
      43. Jablonskia
      44. Baccaurea

45. Apodiscus
46. Ashtonia
47. Aporusa

6d. Subtribe ANTIDESMINAE
48. Thecacoris
49. Phyllanoa
50. Celianella
51. Leptonema
52. Antidesma
53. Hyeronima

6e. Subtribe PORANTHERINAE
54. Poranthera
55. Oreoporanthera

7. Tribe HYMENOCARDIEAE
56. Didymocistus
57. Hymenocardia

8. Tribe BISCHOFIEAE
58. Bischofia

Incertae Sedis (within Phyllanthoideae)
59. Centroplacus
60. Meborea

II. Subfamily OLDFIELDIOIDEAE

9. Tribe CROIZATIEAE
61. Croizatia

10. Tribe PODOCALYCEAE

10a. Subtribe PODOCALYCINAE
62. Podocalyx

10b. Subtribe TETRACOCCINAE
63. Tetracoccus

10c. Subtribe PARADRYPETINAE
64. Paradrypetes

11. Tribe CALETIEAE

11a. Subtribe HYAENANCHINAE
65. Hyaenanche

11b. Subtribe DISSILARIINAE
66. Austrobuxus
67. Dissiliaria
68. Canaca
69. Whyanbeelia
70. Choriceras
71. Longetia

11c. Subtribe PETALOSTIGMATINAE
72. Petalostigma

11d. Subtribe PSEUDANTHINAE
73. Kairothamnus
74. Scagea
75. Neoroepera
76. Micrantheum
77. Pseudanthus
78. Stachystemon

12. Tribe PICRODENDREAE

12a. Subtribe PICRODENDRINAE
79. Celaenodendron
80. Piranhea
81. Picrodendron
82. Parodiodendron

12b. Subtribe PAIVAEUSINAE
83. Oldfieldia

12c. Subtribe MISCHODONTINAE
84. Aristogeitonia
85. Mischodon
86. Voatomalo
87. Androstachys
88. Stachyandra

III. Subfamily ACALYPHOIDEAE

13. Tribe CLUTIEAE
89. Clutia

14. Tribe POGONOPHOREAE
90. Pogonophora

15. Tribe CHAETOCARPEAE
91. Trigonopleura
92. Chaetocarpus

16. Tribe PEREAE
93. Pera

17. Tribe CHEILOSEAE
94. Cheilosa
95. Neoscortechinia

18. Tribe ERISMANTHEAE
96. Erismanthus
97. Moultonianthus
98. Syndyophyllum

19. Tribe DICOELIEAE
99. Dicoelia

20. Tribe GALEARIEAE
100. Microdesmis
101. Galearia
102. Panda

21. Tribe AMPEREAE
103. Monotaxis
104. Amperea

22. Tribe AGROSTISTACHYDEAE
105. Agrostistachys
106. Pseudagrostistachys
107. Cyttaranthus
108. Chondrostylis

23. Tribe CHROZOPHOREAE

23a. Subtribe SPERANSKIINAE
109. Speranskia

23b. Subtribe DITAXINAE
110. Caperonia
111. Philyra
112. Ditaxis
113. Argythamnia
114. Chiropetalum

23c. Subtribe DORYXYLINAE
115. Doryxylon
116. Sumbaviopsis
117. Thyrsanthera
118. Melanolepis

23d. Subtribe CHROZOPHORINAE
119. Chrozophora

24. Tribe CARYODENDREAE
120. Caryodendron
121. Discoglypremna
122. Alchorneopsis

25. Tribe BERNARDIEAE
123. Bernardia
124. Necepsia
125. Paranecepsia
126. Discocleidion
127. Adenophaedra

26. Tribe PYCNOCOMEAE

26a. Subtribe PYCNOCOMINAE
128. Pycnocoma
129. Droceloncia
130. Argomuellera

26b. Subtribe BLUMEODENDRINAE
131. Blumeodendron
132. Podadenia
133. Ptychopyxis
134. Botryophora

27. Tribe EPIPRINEAE

27a. Subtribe EPIPRININAE
135. Epiprinus
136. Symphyllia

137. Adenochlaena
138. Cleidiocarpon
139. Koilodepas
140. Cladogynos
141. Cephalocrotonopsis
142. Cephalocroton

27b. Subtribe CEPHALOMAPPINAE
143. Cephalomappa

28. Tribe ADELIEAE
144. Adelia
145. Crotonogynopsis
146. Enriquebeltrania
147. Lasiocroton
148. Leucocroton

29. Tribe ALCHORNEAE
29a. Subtribe ALCHORNEINAE
149. Orfilea
150. Bossera
151. Alchornea
152. Coelebogyne
153. Aparisthmium
154. Bocquillonia

29b. Subtribe CONCEVEIBINAE
155. Conceveiba
156. Gavarretia
157. Polyandra

30. Tribe ACALYPHEAE
30a. Subtribe RICININAE
158. Ricinus

30b. Subtribe ADRIANINAE
159. Adriana

30c. Subtribe MERCURIALINAE
160. Mercurialis
161. Seidelia
162. Leidesia

30d. Subtribe DYSOPSIDINAE
163. Dysopsis

30e. Subtribe CLEIDIINAE
164. Wetria
165. Cleidion
166. Sampantaea

30f. Subtribe MACARANGINAE
167. Macaranga

30g. Subtribe CLAOXYLINAE
168. Erythrococca
169. Claoxylon
170. Claoxylopsis
171. Mareya
172. Discoclaoxylon
173. Micrococca
174. Amyrea

30h. Subtribe LOBANILIINAE
175. Lobanilia

30i. Subtribe ROTTLERINAE
176. Mallotus
177. Deuteromallotus
178. Cordemoya
179. Coccoceras
180. Trewia
181. Neotrewia
182. Rockinghamia
183. Octospermum

30j. Subtribe ACALYPHINAE
184. Acalypha

30k. Subtribe LASIOCOCCINAE
185. Lasiococca
186. Spathiostemon
187. Homonoia

31. Tribe PLUKENETIEAE
31a. Subtribe PLUKENETIINAE
188. Haematostemon
189. Astrococcus
190. Angostyles
191. Romanoa
192. Eleutherostigma
193. Plukenetia
194. Vigia

31b. Subtribe TRAGIINAE
195. Cnesmone
196. Megistostigma
197. Sphaerostylis
198. Tragiella
199. Platygyna
200. Tragia
201. Acidoton
202. Pachystylidium

31c. Subtribe DALECHAMPIINAE
203. Dalechampia

32. Tribe OMPHALEAE
204. Omphalea

IV. Subfamily CROTONOIDEAE
33. Tribe MICRANDREAE
33a. Subtribe MICRANDRINAE
205. Micrandra
206. Micrandropsis
207. Cunuria

33b. Subtribe HEVEINAE
208. Hevea

34. Tribe MANIHOTEAE
209. Manihot
210. Cnidoscolus

35. Tribe ADENOCLINEAE
35a. Subtribe ADENOCLININAE
211. Glycydendron
212. Klaineanthus
213. Tetrorchidium
214. Adenocline
215. Ditta

35b. Subtribe ENDOSPERMINAE
216. Endospermum

36. Tribe GELONIEAE
217. Suregada

37. Tribe ELATERIOSPERMEAE
218. Elateriospermum

38. Tribe JATROPHEAE
219. Jatropha
220. Vaupesia
221. Oligoceras
222. Deutzianthus
223. Joannesia
224. Leeuwenbergia
225. Annesijoa

39. Tribe CODIAEAE
226. Baloghia
227. Hylandia
228. Ostodes
229. Pausandra
230. Dodecastigma
231. Pantadenia
232. Dimorphocalyx
233. Fontainea
234. Codiaeum
235. Sphyranthera
236. Acidocroton
237. Blachia
238. Strophioblachia

239. Sagotia
240. Baliospermum

40. Tribe TRIGONOSTEMONEAE
241. Trigonostemon

41. Tribe RICINOCARPEAE
41a. Subtribe RICINOCARPINAE
242. Ricinocarpos
243. Alphandia
244. Beyeria
41b. Subtribe BERTYINAE
245. Bertya
246. Myricanthe
247. Cocconerion
248. Borneodendron

42. Tribe CROTONEAE
249. Mildbraedia
250. Fahrenheitia
251. Moacroton
252. Croton

43. Tribe RICINODENDREAE
253. Givotia
254. Ricinodendron
255. Schinziophyton

44. Tribe ALEURITIDEAE
44a. Subtribe ALEURITINAE
256. Aleurites
257. Reutealis
258. Vernicia
44b. Subtribe GARCIINAE
259. Garcia
44c. Subtribe GROSSERINAE
260. Cavacoa
261. Grossera
262. Tapoides
263. Anomalocalyx
264. Sandwithia
265. Tannodia
266. Domohinea
44d. Subtribe CROTONOGYNINAE
267. Cyrtogonone
268. Crotonogyne
269. Manniophyton
44e. Subtribe NEOBOUTONINAE
270. Neoboutonia
271. Benoistia

V. Subfamily EUPHORBIOIDEAE
45. Tribe STOMATOCALYCEAE
45a. Subtribe STOMATOCALYCINAE
272. Plagiostyles
273. Pimelodendron
45b. Subtribe HAMILCOINAE
274. Hamilcoa
275. Nealchornea

46. Tribe HIPPOMANEAE
46a. Subtribe MABEINAE
276. Mabea
277. Senefeldera
278. Senefelderopsis
46b. Subtribe CARUMBIINAE
279. Omalanthus
46c. Subtribe HIPPOMANINAE
280. Spirostachys
281. Sebastiania
282. Stillingia
283. Gymnanthes
284. Excoecaria
285. Colliguaja
286. Dalembertia
287. Adenopeltis
288. Sapium
289. Glyphostylus
290. Grimmeodendron
291. Bonania
292. Duvigneaudia
293. Maprounea
294. Hippomane

47. Tribe PACHYSTROMATEAE
295. Pachystroma

48. Tribe HUREAE
296. Tetraplandra
297. Algernonia
298. Ophthalmoblapton
299. Hura

49. Tribe EUPHORBIEAE
49a. Subtribe ANTHOSTEMINAE
300. Anthostema
301. Dichostemma
49b. Subtribe NEOGUILLAUMINIINAE
302. Neoguillauminia
303. Calycopeplus
49c. Subtribe EUPHORBIINAE
304. Euphorbia
305. Chamaesyce
306. Cubanthus
307. Monadenium
308. Synadenium
309. Endadenium
310. Pedilanthus

Incertae Sedis (within Euphorbiaceae)
311. Chlamydojatropha
312. Martretia
313. Tacarcuna
314. Avellanita
315. Cubacroton
316. Dendrothrix
317. Cladogelonium

APPENDIX 2. List of new taxa.

CROIZATIEAE Webster, trib. nov.
LEPTOPINAE Webster, subtr. nov.
PODOCALYCEAE Webster, trib. nov.
PODOCALYCINAE Webster, subtr. nov.
PYCNOCOMINAE Webster, subtr. nov.
TETRACOCCINAE Levin, subtr. nov.
DALECHAMPIINAE (Muell. Arg.) Webster, stat. nov.
PICRODENDRINAE (Small) Webster, stat. nov.
PORANTHERINAE (Muell. Arg.) Webster, stat. nov.
SCEPINAE (Lindl.) Webster, stat. nov.
SPONDIANTHINAE (Webster) Webster, stat. nov.
Acidocroton sect. Ophellantha (Standl.) Webster, comb. nov.
Acidocroton spinosus (Standl.) Webster, comb. nov.
Acidocroton steyermarkii (Standl.) Webster, comb. nov.
Adenopeltis serrata (Ait.) Webster, comb. nov.
Deutzianthus thyrsiflorus (Airy Shaw) Webster, comb. nov.
Gymnanthes schomburgkii (Kl.) Webster, comb. nov.
Leptopus diplospermus (Airy Shaw) Webster, comb. nov.
Leptopus phyllanthoides (Nutt.) Webster, comb. nov.
Lingelsheimia manongarivensis (Leandri) Webster, comb. nov.
Orfilea multispicata (Baillon) Webster, comb. nov.
Orfilea neraudiana (Baillon) Webster, comb. nov.
Pantadenia chauvetiae (Leandri) Webster, comb. nov.

Phyllanthus anamalayanus (Gamble) Webster, comb. nov.
Phyllanthus chevalieri (Gagnep.) Webster, comb. nov.
Sauropus pierrei (Beille) Webster, comb. nov.

APPENDIX 3. *Index to genera and higher taxa.* This index includes all the genera and higher taxa mentioned in this paper. Accepted taxa are shown in bold, with suprageneric taxa all capitalized. Synonymized taxa are italicized, and those merely mentioned are shown in regular text. Taxa are numbered as they appear in the text, with those in Roman numerals referring to subfamilies, those preceded by "T" referring to tribes or subtribes, those preceded by "E" referring to excluded taxa, and others referring to genera.

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SYSTEMATICS OF THE EUPHORBIACEAE

The first International Conference on the Systematics of the Euphorbiaceae was held at the Missouri Botanical Garden in St. Louis on 14–16 August 1989. Papers were presented by 21 people (several of these with one or more collaborators); of these, 15 authors submitted papers that were accepted for publication and are presented in this issue and the one preceding.

Support for the conference and for the publication of its proceedings was provided by National Science Foundation Grant BSR-8817991. The published papers benefitted from the editorial assistance and scientific reviews of Michael J. Huft, Geoffrey A. Levin, and Grady L. Webster.

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THE CONTRIBUTION OF EMBYROLOGY TO THE SYSTEMATICS OF THE EUPHORBIACEAE[1]

R. N. Kapil[2] *and A. K. Bhatnagar*[2]

Abstract

The Euphorbiaceae are often described as a heterogeneous group with ambiguous affinities. Although their vegetative and floral characters are markedly modified in relation to the habitat and pollination mechanisms, the embryological features are comparatively more conservative, and therefore quite useful in the delimitation of as well as in understanding of relationships. The diagnostic embryological characteristics of the family are: (1) tetrasporangiate anther, 4- or 5-layered anther wall, fibrous endothecium, ephemeral middle layer(s), secretory tapetum with multinucleate cells, simultaneous cytokinesis, tetrahedral, decussate and isobilateral microspore tetrads, and 2- or 3-nucleate pollen; (2) tricarpellary, syncarpous, and trilocular ovary with one or two ovules in each locule, axile placentation, anatropous or hemianatropous, bitegmic, crassinucellate ovule, placental obturator and presence of hypostase; (3) embryo sac with ephemeral antipodal cells, nuclear endosperm and mature embryo with broad/leafy cotyledons; and (4) albuminous seed with both integuments forming seed coat, and outer epidermis of inner integument developing into a fibrous or sclerotic layer. Most of the 30 families included in the Euphorbiales by various authors have significant embryological differences from Euphorbiaceae. It appears more appropriate that the Euphorbiales should include only one family, the Euphorbiaceae. The closeness of the Euphorbiales with the Malvales finds support on embryological grounds. The present level of embryological information substantiates the classification of the Euphorbiaceae into five subfamilies. It seems that the Acalyphoideae diverged rather early from the Phyllanthoideae–Oldfieldioideae, and later the Crotonoideae and the Euphorbioideae evolved as independent lines from the Acalyphoideae. Since only 16 of the 50 tribes have so far been embryologically explored, comments on the tribal classification must await further probes into their reproductive biology.

The Euphorbiaceae represent a large group of flowering plants distributed in almost all parts of the world, except the arctic regions. The family includes 300 genera and 8000 species (Webster, 1987a) predominantly distributed in the tropical and subtropical areas of both the New and Old Worlds. Because of the great variability in vegetative and floral characters, the group has been described as heterogeneous and highly diversified (Webster, 1967; Corner, 1976).

It is being increasingly realized that a natural or phylogenetic classification, be it of the angiosperms as a whole, or of a class, order, or family, cannot be based solely on morphological characters. The external features are often drastically modified in relation to environmental stress and fail to reflect true phyletic trends. Embryology has, therefore, acquired an important place, along with other disciplines such as cytology, anatomy, palynology, and chemotaxonomy, as a dependable tool in systematics. Embryological features are especially significant in situations where exomorphology either leads to inconclusive correlations or may even delude due to convergence (Kapil & Bhatnagar, 1980). Wagenitz (1975) rightly emphasized that "for elucidation of the systematic position of groups with simple flowers embryological and phytochemical characters are especially valuable, as classical characters of flower may be too seriously altered by reduction." The embryological characters have also proved useful in: (i) determining the limits of a taxon, especially at the level of a family or order; (ii) ascertaining affinities when two or more possibilities are suspected; and (iii) evaluating a scheme of classification.

In the Euphorbiaceae, the sporophytic characters exhibit tremendous diversity. They help in recognizing natural groups down to the level of species and even below. On the other hand, the highly reduced gametophytic generations display much less variability. They are quite uniform at the generic level and above. They are more convincing not only in circumscribing the family, but also in judging its affiliations and in classifying it into subfamilies and tribes.

Considering the large size, the Euphorbiaceae are embryologically poorly known. Only 16 tribes (and about 30 genera), out of 50 tribes recognized

We thank Michael J. Huft, Geoffrey A. Levin, and two anonymous reviewers for comments and suggestions.

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by Webster (1987a; 1989, privately circulated), have been investigated. Some genera of economic importance, e.g., *Ricinus* L. and *Hevea* Aublet, and others of horticultural interest, e.g., *Acalypha* L., *Jatropha* L., and *Euphorbia* L., are well studied (see Table 1). It seems that the choice of the investigated species has depended on the availability of research material rather than on systematic considerations.

In the Phyllanthoideae, *Putranjiva* Wall., *Phyllanthus* L., *Breynia* J. R. & G. Forster, and *Bischofia* Blume are embryologically well known, whereas *Agyneia* L., *Meineckia* Baillon, *Sauropus* Blume, and *Securinega* Juss. are partially understood. The Oldfieldioideae are almost unknown except for some information on the ovule and seed of *Micrantheum* Desf. and *Androstachys* Prain, and the pollen and ovule of *Picrodendron* Planch. Subfamily Acalyphoideae, with 18 tribes, is familiar to the embryologist through studies on nine genera belonging to three tribes, viz. *Chrozophora* A. Juss. of Chrozophoreae, *Mallotus* Lour., *Mercurialis* L., *Ricinus*, *Micrococca* Benth., *Trewia* L., and *Acalypha* of Acalphyeae, and *Tragia* L. and *Dalechampia* L. of Plukenetieae. In the Crotonoideae, which have been subdivided into 13 tribes by Webster (1987a; 1989, privately circulated), only seven genera belonging to six tribes have been explored. These are *Hevea*, *Manihot* Mill., *Jatropha*, *Codiaeum* A. Juss., *Croton* L., *Baliospermum* Blume, and *Aleurites* J. R. & G. Forster. In the Euphorbioideae, a disproportionately large body of embryological data are available for *Euphorbia*. The only other genera that have been investigated are *Sebastiania* Sprengel and to some extent *Sapium* P. Browne, *Excoecaria* L., and *Hura* L.

The paucity of embryological data can be partly ascribed to the difficulty in collecting a close series of developmental stages of buds, flowers, and fruits. The processing of material, sectioning, and staining are laborious and time-consuming procedures. In spite of these limitations, embryology has helped to solve some controversies (see Kapil & Bhatnagar, 1980). More and more taxonomists are taking embryological information into account when suggesting new schemes of classification and taxonomic relationships (see Dahlgren, 1975, 1980; Takhtajan, 1980; Cronquist, 1981; Thorne, 1983; Goldberg, 1986).

The main objective of this contribution is to document the ways in which embryology has contributed toward deciding the status of the Euphorbiaceae in the Euphorbiales, elucidating affinities of the Euphorbiaceae, and in determining how best this family can be classified into subfamilies.

Embryological Characters of the Euphorbiaceae

The following set of correlated embryological features (see Wunderlich, 1967; Kapil & Bhatnagar, 1972; Webster & Rupert, 1973) characterizes the Euphorbiaceae:

1. Tetrasporangiate anther, 4- or 5-layered anther wall, fibrous thickenings in endothecium, ephemeral middle layer(s), single layered tapetum of secretory type, bi- or multinucleate tapetal cells, often with lobed multinucleolate nuclei, simultaneous cytokinesis, tetrahedral, decussate or isobilateral microspore tetrads, 2- or 3-nucleate pollen grains.
2. Tricarpellary, syncarpous, trilocular ovary with two (Phyllanthoideae and Oldfieldioideae) or one (Acalyphoideae, Crotonoideae and Euphorbioideae) ovules in each locule, axile placentation, anatropous or hemianatropous, bitegmic, crassinucellate ovules, ventral raphe, funicular vascular supply terminating in chalaza or entering the base of nucellus or integuments, placental obturator, well-differentiated hypostase, hypodermal single or multicelled achesporium, female gametophyte with ephemeral antipodal cells, fusion of polar nuclei near egg apparatus.
3. Primary endosperm nucleus dividing earlier than zygote, nuclear endosperm, embryo with large leafy cotyledons.
4. Seed with copious endosperm containing oil and starch, persistence of hypostase in the seed, formation of seed coat by both integuments, outer epidermis of inner integument differentiating into mechanical palisade or fibrous layer, and proliferative tip of outer integument often producing the caruncle.

Distribution of Some Embryological Characters in the Euphorbiaceae

1. Pollen nuclear number. There is an interesting assortment of distribution of 2- and 3-nucleate pollen grains in the Euphorbiaceae. *Euphorbia* is one of the five exceptional angiosperm genera in which both 2- and 3-nucleate pollen grains occur in different species (Brewbaker, 1967; Webster & Rupert, 1973). In his study, which included 17 genera (35 species) of the Euphorbiaceae, Brewbaker (1967) observed that 13 genera had 2-nucleate pollen, 3 had 3-nucleate and only 1 had species with 2- or 3-nucleate pollen. Among 16 species of *Euphorbia* investigated, some species had 2-nucleate and others 3-nucleate pollen grains. He concluded that the distribution of 2- and

TABLE 1. Embryological studies in the Euphorbiaceae. +: presence; −: absence.

Genus (tribe)	Author(s)	Anther	Ovule	Embryo sac	Endosperm	Embryo	Seed
Phyllanthoideae (11 tribes)							
Putranjiva Wallich (Drypeteae)	Dutt (1942); Banerji & Dutt (1944); R. P. Singh (1970a)	+	+	+	+	−	+
Neopeltandra Gamble (= *Meineckia* Baillon) (Phyllantheae)	P. N. Rao (1970); Venkateswarlu et al. (1973)	+	+	−	−	−	−
Securinega Juss. (Phyllantheae)	Bhatnagar & Kapil (unpublished); Corner (1976)	−	+	+	−	−	+
Breynia J. R. & G. Forster (Phyllantheae)	Thathachar (1953b); Venkateswarlu et al. (1973); Corner (1976)	+	+	+	+	+	+
Melanthesa Blume (= *Breynia* J. R. & G. Forster) (Phyllantheae)	R. P. Singh (1968)	−	+	−	+	+	+
Agyneia L. (= *Glochidion* J. R. & G. Forster) (Phyllantheae)	Mukherjee (1962); Corner (1976)	+	+	+	−	−	+
Phyllanthus L. (Phyllantheae)	R. P. Singh (1956, 1972); Dang-Van-Liem (1962); Mukherjee & Padhye (1964); Chopra & Singh (1969)	+	+	+	+	+	+
Sauropus Blume (Phyllantheae)	P. N. Rao (1970)	+	+	−	−	−	−
Bischofia Blume (Bischofieae)	Bhatnagar & Kapil (1973, 1979); Corner (1976)	+	+	+	+	+	+
Oldfieldioideae (3 tribes)							
Androstachys Prain (Picrodendreae)	Dahlgren & van Wyk (1988)	−	+	−	−	−	+
Picrodendron Planchon (Picrodendreae)	Hayden et al. (1984); Hakki (1985)	−	+	−	−	−	−
Micrantheum Desf. (Caletieae)	Berg (1975)	−	+	−	−	−	+
Acalyphoideae (18 tribes)							
Chrozophora A. Juss. (Chrozophoreae)	Kapil (1956a, b); Dang-Van-Liem (1962); Bor & Kapil (1976)	+	+	+	+	+	+
Ricinus L. (Acalypheae)	R. P. Singh (1954); Dang-Van-Liem (1962)	−	+	−	+	+	+
Micrococca Bentham (Acalypheae)	P. N. Rao (1962); Nair & Abraham (1963)	+	+	+	+	+	+
Acalypha L. (Acalypheae)	Tateishi (1927); Landes (1946); Thathachar (1952); Johri & Kapil (1953); Kapil (1960); Mukherjee (1958, 1964)	+	+	+	+	+	+
Mercurialis L. (Acalypheae)	Dang-Van-Liem (1962); Corner (1976)	−	−	−	−	+	+
Mallotus Loureiro (Acalypheae)	Ventura (1934); Thathachar (1953a); Raju & Rao (1953)	+	+	+	+	+	−
Trewia L. (Acalypheae)	Banerji & Dutt (1944)	−	+	+	−	−	−
Tragia L. (Plukenetieae)	Mukherjee (1962, 1968); Nair & Abraham (1980)	+	+	+	−	−	−
Dalechampia L. (Plukenetieae)	R. P. Singh & Pal (1968); G. L. Webster & B. D. Webster (1972)	−	+	+	+	+	+

TABLE 1. Continued.

Genus (tribe)	Author(s)	Anther	Ovule	Embryo sac	Endosperm	Embryo	Seed
Crotonoideae (13 tribes)							
Hevea Aublet (Micrandreae)	Muzik (1954); Bouharmont (1962); A. N. Rao (1964)	−	+	+	+	+	+
Manihot Miller (Manihoteae)	P. N. Rao & Sarveswara Rao (1976); Dang-Van-Liem (1962); Corner (1976)	−	−	−	−	+	+
Jatropha L. (Jatropheae)	Mukherjee (1962); R. P. Singh (1970b)	+	+	+	−	−	+
Baliospermum Blume (Codiaeae)	P. N. Rao (1970)	+	+	−	−	−	−
Codiaeum A. Juss. (Codiaeae)	Galimberti (1963); R. P. Singh (1965); Bor & Bouman (1974)	−	+	+	+	−	+
Croton L. (Crotoneae)	Thathachar (1953b); Venkateswarlu & Rao (1963); R. P. Singh & Chopra (1970)	+	+	+	+	+	+
Aleurites J. R. & G. Forster (Aleuritidae)	Wiehr (1930); McCann (1945); Sharma (1955)	+	+	+	−	−	+
Euphorbioideae (5 tribes)							
Excoecaria L. (Hippomaneae)	P. N. Rao (1970)	+	+	−	−	−	−
Sapium P. Browne (Hippomaneae)	Chopra (1970); Corner (1976)	−	+	+	−	−	+
Sebastiania Sprengel (Hippomaneae)	Thathachar (1953b); Nair & Maitreyi (1962)	+	+	+	+	+	+
Hura L. (Hureae)	P. N. Rao (1970)	+	+	−	−	−	−
Euphorbia L. (Euphorbieae)	Kapil (1961); R. P. Singh & Jain (1965); R. P. Singh (1969); Bor & Kapil (1975); Battaglia (1986)	+	+	+	+	+	+

3-nucleate pollen within the Euphorbiaceae was random.

Webster & Rupert (1973) investigated 66 species belonging to 42 genera. They found a definite phylogenetic pattern in the distribution of 2- and 3-nucleate pollen. For example, the biovulate subfamilies Phyllanthoideae and Oldfieldioideae had 2-nucleate pollen in 14 genera. Among the uniovulate subfamilies, the Acalyphoideae showed the 2-nucleate condition. In the Crotonoideae, 2-nucleate pollen grains are found in a larger number of tribes (Jatropheae, Gelonieae, Codiaeae, Ricinocarpeae, Aleuritideae, Neoboutonieae) and 3-nucleate in fewer (Micrandreae, Manihoteae, Crotoneae). In the Euphorbioideae (sensu Webster, 1987a) both the large tribes Hippomaneae and Euphorbieae have 2- and 3-nucleate genera (Webster et al., 1982).

In angiosperms, the 2-nucleate condition of pollen is considered primitive and 3-nucleate advanced. The shift from the 2-nucleate to 3-nucleate condition is regarded as irreversible (Webster & Rupert, 1973; Goldberg, 1986). It therefore seems that in the Euphorbiaceae the 3-nucleate condition has evolved independently, perhaps more than once, in the Crotonoideae and Euphorbioideae.

2. Integument initiation in the ovule. Carpellary and ovular characteristics in the Euphorbiaceae have been considered to be rather uniform (Webster, 1967; Cronquist, 1988). However, an interesting variation is seen in the pattern of integument initiation among various subfamilies. In angiosperms, the bitegmic ovules usually have their inner integument derived from the dermal layer and the outer chiefly from subdermal cells of the ovular primordium (Bouman, 1974). Bor & Bouman (1974) and Bor & Kapil (1975, 1976) noticed the unique occurrence of subdermal initiation of both inner and outer integuments in *Euphorbia milii* Des Moulins, *E. geniculata* Orteg. (Euphorbioideae), *Codeiaeum variegatum* Blume (Crotonoideae), and *Crozophora obliqua* A. Juss. (Acalyphoideae). In *Bischofia javanica* Blume (Kapil & Bhatnagar, 1980) and *Securinega leucopyrus* (Willd.) Muell.-Arg. (unpublished obs.) both

of the integuments are initiated by divisions in dermal cells of the ovular primordium. Thus, the biovulate Phyllanthoideae differ prominently from the uniovulate subfamilies of the Euphorbiaceae. Corresponding details, yet unknown for the Oldfieldioideae, would be significant.

In the Phyllanthoideae, with dermal initiation of both integuments, the subdermal cells, too, contribute to the development of the core of the thickened base of the integuments, particularly of the outer one. Similarly, in the Acalyphoideae, Crotonoideae, and Euphorbioideae, which have subdermal initiation of the integuments, the epidermal layer of each integument divides to form the apical portions (rim) of the integuments. It is therefore quite likely that the dermal integuments of the Phyllanthoideae and subdermal integuments of the Acalyphoideae, Crotonoideae, and Euphorbioideae owe their origin to a common ancestral condition in which both dermal and subdermal cells contributed to the development of the integuments.

3. Nucellar beak, nucellar cap, and obturator. A majority (*Phyllanthus*, Mukherjee & Padhye, 1964; *Melanthesa*, R. P. Singh, 1968; *Sauropus*, *Breyenia*, P. N. Rao, 1970; *Securinega*, unpublished obs.) of the Phyllanthoideae have a well developed nucellar beak that projects beyond the integuments and comes in contact with the obturator outside the micropyle. The beak is produced by divisions in both the parietal tissue and the dermal layer of the apical part of nucellus. Venkateswarlu et al. (1973) illustrated ovules with prominent nucellar beaks in *Meineckia parviflora* (Wight) Webster, *Chorisandra pinnata* Wight, and other Phyllanthoideae. In *Bischofia* the nucellus has an active micropylar axial tissue derived from the parietal cell. The epidermal layer also divides periclinally and anticlinally to contribute to the prominent nucellar cap, which does not extend beyond the micropyle. *Putranjiva roxburghii* Wall. (R. P. Singh, 1970a) is, however, an exception within the Phyllanthoideae in which the upper portion of the nucellus is reported to be insignificant and ephemeral. *Micrantheum* and *Picrodendron* of the Oldfieldioideae (Berg, 1975; fig. 29 in Hakki, 1985) also show a prominent nucellar cap derived by divisions in both the dermal and subdermal cells of the nucellus. The Acalyphoideae (*Micrococca*, Nair & Abraham, 1963; *Acalypha*, Banerji, 1949, Mukherjee, 1962; *Chrozophora*, Bor & Kapil, 1976) have a prominent nucellar beak derived from both dermal and subdermal cells. The beak extends far beyond the micropyle in *Chrozophora*. In *Dalechampia* (R. P. Singh & Pal, 1968; G. L. Webster & B. D. Webster, 1972) and *Tragia* (Mukherjee, 1962) it grows up to the exostome, whereas in *Ricinus* (R. P. Singh, 1954), *Mallotus* (Thathachar, 1953a), *Micrococca*, and *Acalypha* it does not cross the endostome. The Crotonoideae (*Jatropha*, Mukherjee, 1962; *Codiaeum*, Bor & Bouman, 1974; *Baliospermum*, P. N. Rao, 1970), too, are characterized by the presence of a prominent nucellar beak. In the Euphorbioideae the extent of nucellar development shows far more variation. A large number of them (*Hura*, P. N. Rao, 1970; *Sapium*, Chopra, 1970; *Sebastiania*, Nair & Maitreyi, 1962) possess a well-developed nucellar cap that does not extend outside the micropyle. In *Euphorbia*, some species (e.g., *E. hypericifolia* L., Mukherjee, 1957; *E. helioscopia* L., R. P. Singh, 1969) have a long nucellar beak, whereas others (e.g., *E. geniculata*, Bor & Kapil, 1975; *E. milii*, Bor & Bouman, 1974; *E. peltata* Roxb., Mukherjee, 1965) have a short beak or a nucellar cap that does not extend beyond the micropyle.

Presence of a nucellar beak in the Euphorbiaceae is more widespread and seems to represent the primitive state of the character. The beak extends out of the micropyle and comes in contact with the obturator. Reduction in size of the nucellus (so that it is in the form of a cap which does not extend beyond the micropyle) is correlated with more extensive development of the obturator. In fact, in ovules with a projecting nucellar beak the obturator is small and its cells are compactly arranged. On the other hand, when the nucellus is smaller in extent, the obturator is prominent and its trichomelike epidermal cells project into the micropyle and come in contact with the nucellar tip. Both obturator and the nucellar beak/cap are supposed to be involved in the nutrition of the pollen tube as well as in guiding it to the embryo sac. Their correlated development is, therefore, complementary.

4. Ontogeny of the female gametophyte. The monosporic, 8-nucleate female gametophyte of the *Polygonum* type characterizes over 80 per cent of the investigated angiosperms (Maheshwari, 1950) and is therefore regarded as the primitive state. In the Euphorbiaceae, the Phyllanthoideae (*Phyllanthus*, *Putranjiva*, *Bischofia*) have the *Polygonum* type of female gametophyte. Information on female gametophytes is lacking in the Oldfieldioideae. In the Acalyphoideae, *Chrozophora*, *Micrococca*, and *Dalechampia* have the *Polygonum* type of female gametophyte, whereas *Acalypha* (Tateishi, 1927; Mukherjee, 1958; Johri & Kapil, 1953; Kapil,

1960) and *Mallotus* species (Ventura, 1934; Thathachar, 1953a) have tetrasporic embryo sacs of *Penaea*, *Acalypha indica*, *Peperomia hispidula*, or *Drusa* types. The Crotonoideae (*Codiaeum*, *Jatropha*), too, are reported to have only the *Polygonum* type of embryo sac. In the Euphorbioideae, *Sebastiania* and *Sapium* have the *Polygonum* type of embryo sac. However, the genus *Euphorbia* is unique. While a majority of its species (e.g., *E. geniculata*, *E. milii*, *E. heterophylla* L., and *E. pilosa* L.) have the *Polygonum* type of embryo sac, others show tetrasporic, *Fritillaria/Euphorbia dulcis* type (*E. dulcis*; Kapil, 1961; Battaglia, 1986) or *Penaea* type (*E. palustris* L.; Modilewski, 1911).

It thus seems obvious that a *Polygonum* type of embryo sac represents the primitive state in the Euphorbiaceae. From this, the tetrasporic type appears to have evolved independently in some Acalyphoideae and Euphorbioideae.

5. Development of endosperm. Irrespective of the number of nuclei participating in the formation of the primary endosperm nucleus, the basic pattern of development and behavior of endosperm is remarkably uniform in the Euphorbiaceae (see Kapil & Bhatnagar, 1972). The primary endosperm nucleus divides earlier than the zygote. Free nuclear divisions continue until 32–256 nuclei are produced. Wall formation is usually initiated at the globular or heart-shaped stages of the proembryo. It usually begins at the micropylar end and later extends along the periphery of the embryo toward the chalazal end (e.g., in *Ricinus*, *Aleurites*, *Hevea*, *Chrozophora*, *Micrococca*, *Sebastiania*, *Euphorbia*) or the wall may be laid down simultaneously along the periphery of the embryo sac (in *Acalypha*; Johri & Kapil, 1953). Wall formation extends centripetally until the entire endosperm becomes cellular. The first formed endosperm cells divide periclinally so that tiers of radially arranged cells are produced.

Of the large number of taxa investigated, only three species of *Croton* —*C. sparsiflorus* Morong (= *C. bonplandianum* Baill.), *C. klotzschianus* Gamble (Venkateswarlu & Rao, 1963), and *C. oblongifolius* Roxb. (Pal, 1972)—are known to form free nuclear chalazal endosperm haustorium. Initiated as a small protrusion at the 4- or 8-nucleate stage, it gradually develops into an elongate structure. Simultaneously, free nuclear divisions continue and the nuclei are dispersed peripherally with greater accumulation in the micropylar part. Cell formation is restricted to the micropylar part of the embryo sac, whereas the chalazal portion forms a free nuclear caecumlike structure, which sometimes attains a length of 1000 μm and behaves as an aggressive chalazal haustorium.

The presence of endosperm haustorium is a specialized feature that seems to have evolved only in the advanced Crotonoideae (*Croton* spp.).

6. Caruncle. In several Euphorbiaceae the apical part of the outer integument proliferates after fertilization to produce a soft and fleshy structure, the caruncle, around the micropyle. Its cells enlarge and may be parenchymatous (*Chrozophora*; Bor & Kapil, 1976) or their basal peripheral cells may develop into stone cells (*Micrantheum*; Berg, 1975). The caruncle has been regarded as useful in seed dispersal by ants (Berg, 1975), but its role in exerting stress for opening the locule, in the explosive dispersal of seeds (see Beer & Swaine, 1977), and in facilitating the process of seed germination by absorption of water, deserves further attention.

In the Phyllanthoideae, many of which are trees with drupaceous fruit, the seeds are mostly without a caruncle (*Phyllanthus*, *Putranjiva*, *Melanthesa*, *Sauropus*, *Bischofia*). In the Oldfieldioideae the seeds are described as "often carunculate" (Webster, 1987a). However, Berg (1975) described a well-developed caruncle in *Micrantheum*. In the Acalyphoideae a large majority (e.g., *Chrozophora*, *Acalypha*, *Ricinus*) have carunculate seeds, but a few such as *Dalechampia* lack a caruncle (Webster & Webster, 1972). Curiously, in *Acalypha indica* seeds of the lateral flowers in the inflorescence are carunculate, whereas the single seed of the terminal flower is ecarunculate (Johri & Kapil, 1953). In the Crotonoideae, too, the majority (e.g., *Jatropha*, *Codiaeum*, *Croton*) of investigated taxa have a caruncle. In the Euphorbioideae a caruncle is present in seeds of *Sebastiania* (Nair & Maitreyi, 1962), but is absent in *Excoecaria* (P. N. Rao, 1970) of the same tribe Hippomaneae. In *Euphorbia* some species have a well-developed caruncle (i.e., *E. dulcis*, Kapil, 1961), whereas others have an inconspicuous structure on the ventral micropylar side (*E. milii*, Bor & Bouman, 1974; *E. geniculata*, Bor & Kapil, 1975).

In the Phyllanthoideae the outer integument is dermal in origin and remains 2–4 cell layers thick. As observed in *Phyllanthus* spp. (Mukherjee & Padhye, 1964), *Melanthesa rhamnoides* Wight (R. P. Singh, 1968) and *Bischofia javanica* (Bhatnagar & Kapil, 1973; Bhatnagar, 1978) the tip of the outer integument does not proliferate so that the seed is ecarunculate. In *Micrantheum* of the

Oldfieldioideae the caruncle is produced primarily by divisions of the inner dermal layer at the apical region of the outer integument (Berg, 1975). In Acalyphoideae, Crotonoideae, and Euphorbioideae the outer integument is subdermal in origin (Bor & Bouman, 1974; Bor & Kapil, 1976). The caruncle is formed by proliferation of both subdermal and dermal apical cells of the outer integument. Interestingly, in *Euphorbia geniculata* (Bor & Kapil, 1975) an inconspicuous caruncle develops around the micropyle, on the ventral side of the young seed, by divisions of the dermal cells. In some other species of *Euphorbia* that lack a caruncle, the tip of the outer integument nevertheless shows some proliferation of cells (*Euphorbia milii*; Bor & Bouman, 1974).

It seems, therefore, that formation of a caruncle is a derived feature in the Euphorbiaceae, and its absence in some Euphorbioideae represents the result of secondary loss of this feature.

Circumscription of the Euphorbiales

According to Webster (1987a), "Over 30 families have been included in the Euphorbiales by leading botanists in the 19th and 20th centuries." Of these, the inclusion of the Empetraceae, Stackhousiaceae, Fouquieriaceae, Batidaceae, Gyrostemonaceae, and Nepanthaceae appears to be farfetched. In fact, several taxa, often with simple, unisexual flowers, tricarpellary ovary with one or two ovules in each locule, carunculate seed, and explosive mechanism of seed dispersal were earlier assigned to the Euphorbiaceae or placed close to them. This led to the family acquiring the reputation of a "dust-bin" group. More critical investigations revealed that the resemblance was quite often a result of convergence on account of adaptation to a similar mode of pollination and seed dispersal. Embryological studies, together with evidence from other disciplines such as palynology (Punt, 1962; Köhler, 1965), floral anatomy (V. Singh & Asha Singh, 1975), and wood anatomy (Hayden, 1977; Mennega, 1987) helped in the removal of many alien taxa from the Euphorbiaceae. Only such examples which can possibly have some affinities, and where embryological characters have helped in the circumscription of the family as a more natural group, are considered here.

1. Buxaceae

The boxwoods, because of their simple flowers, tricarpellary ovary, axile placentation, presence of one or two anatropous, bitegmic, and crassinucellate ovules in each locule, and seeds that are sometimes carunculate, were, and still are, often referred close to the Euphorbiaceae (Stebbins, 1974; Bensen, 1979; Cronquist, 1981; Rouleau, 1981). There are some other similarities too; for example, in *Buxus* L. an obturator is present and the ovule has a nucellar cap formed by periclinal divisions in the nucellar epidermis. However, the Buxaceae show many-layered anther tapetum, ovules with a dorsal raphe, dermal inner and subdermal outer integument (see fig. 3D in Wiger, 1935), persistent antipodal cells which even multiply, and fusion of polar nuclei at the chalazal part of the central cell. More important differences lie in the development of endosperm, which is cellular, and seeds, which are exo-mesotestal (Wiger, 1935; Corner, 1976). A report of nuclear endosperm in *Sarcococca* Lindl. needs confirmation. There is thus little justification even for the grouping together of the Buxaceae and the Euphorbiaceae in the same order.

2. Daphniphyllaceae

While most taxonomists now agree that *Daphniphyllum* Blume should be placed in a separate family, disagreement still exists with regard to its affiliations. Emberger (1960), Stebbins (1974), and Rouleau (1981) prefer it to be a part of the Euphorbiales, but Hutchinson (1973), Takhtajan (1980, 1983, 1987), Cronquist (1981), and Goldberg (1986) consider it closer to the Hamamelidales.

Our palynological and embryological investigations of *Daphniphyllum himalayense* Muell. Arg. (Bhatnagar & Garg, 1977; Bhatnagar & Kapil, 1982) assign it a distinctive position from the Euphorbiaceae. This is because it has 3-traced stamens, 8–10 anther wall layers, thickened radial and inner tangential walls of the endothecial cells (without fibrous thickenings), a 2- or 3-layered tapetum, a bicarpellary ovary with two to four parietal ovules, and subdermal outer and dermal inner integument. Moreover, an obturator is absent, the endosperm is cellular, the embryo is small, the seeds have perisperm and are endotegmic and ecarunculate.

Daphniphyllum resembles the Hamamelidales (see Kapil & Kaul, 1972; Kaul & Kapil, 1974) in having an 8-layered anther wall, a bicarpellary, bilocular ovary with incomplete partition, two ovules in each locule, parietal placentation, anatropous, bitegmic, crassinucellate ovules with subdermal outer and dermal inner integument, absence of an obturator, persistent antipodals, cellular endosperm and polyembryony. Nevertheless, it is different from the Hamamelidaceae in having 3-traced stamens

and an endotegmic seed coat. Thus, its inclusion in an independent family Daphniphyllaceae, within the order Hamamelidales or in an independent order Daphniphyllales close to it, appears more satisfactory.

3. SIMMONDSIACEAE

Although there is consensus that *Simmondsia* Nutt. should form an independent family, the Simmondsiaceae, its phylogenetic relationship is still debated. Cronquist (1981, 1988), Thorne (1983), and Dahlgren (1983) place it in the Euphorbiales, whereas others relate it to the Buxaceae (Emberger, 1960), Hamamelidales (Takhtajan, 1983), or the Fagales (Goldberg, 1986).

Simmondsia shares a few embryological traits with the Euphorbiaceae—both have anatropous, bitegmic, crassinucellate ovules and nuclear endosperm. However, it differs from the spurges in having ovules with a dorsal raphe, absence of an obturator and hypostase and in its possessing exomesotestal, exalbuminous seeds. There is no doubt that the Simmondsiaceae are not related to the Euphorbiales, and are perhaps quite out of place in the Buxales or the Hamamelidales as well. Goldberg's (1986) suggestion that *Simmondsia* is related to the Fagales deserves consideration. The presence in both of a 3- to 5-layered anther wall, a nucellar cap, nuclear endosperm, a large vacuole in the chalazal part of the endosperm (see Wiger, 1935; Davis, 1966), exalbuminous, exotestal seeds, and a large, straight embryo with thick cotyledons (Corner, 1976) is indicative of such a relationship.

4. *BISCHOFIA*

Bischofia javanica, a tall deciduous tree, has been placed either in the tribe Phyllantheae or in an independent tribe Bischofeae within the subfamily Phyllanthoideae (Hutchinson, 1969; Webster, 1987a). However, Airy Shaw (1965, 1966) assigned the same genus to an independent family, Bischofiaceae, which he thought was related to the Staphyleaceae.

An embryological study of *Bischofia javanica* (Bhatnagar & Kapil, 1973, 1979; Bhatnagar, 1978) indicated that this species resembles other Phyllanthoideae (Mukherjee & Padhye, 1964; Chopra & Singh, 1969; R. P. Singh, 1970a) even in minute details. The common features are: a 5-layered anther wall, fibrous endothecium, ephemeral middle layers, a secretory tapetum with multinucleate cells, a tricarpellary ovary, two anatropous, bitegmic, crassinucellate ovules with a ventral raphe borne on axile placenta in each locule, dermal integuments (as in *Securinega*), formation of a nucellar cap and placental obturator, differentiation of hypostase, a *Polygonum* type of embryo sac, Onagrad embryogeny, and exotegmic seeds. Hence, the removal of *Bischofia* from the Euphorbiaceae is uncalled for.

5. *PICRODENDRON*

This genus has been variously classified in the Anacardiaceae, Bombacaceae, Burseraceae, Euphorbiaceae, Juglandaceae, Sapindaceae, and Simaroubaceae (see Hakki, 1985). Webster (1987a) treated it as a tribe Picrodendreae in the subfamily Oldfieldioideae of the Euphorbiaceae.

Hakki (1985) studied some aspects of floral morphology and embryology of the West Indies species *Picrodendron baccatum* (L.) Krug & Urban. It certainly resembles the Euphorbiaceae in having two collateral, anatropous, bitegmic and crassinucellate ovules borne on axile placenta, and presence of a nucellar cap, obturator, and hypostase. Based on morphological and palynological features, Hayden et al. (1984) strongly supported an alliance of *Picrodendron* with the Oldfieldioideae. *Picrodendron* is distinct in having a bicarpellary, bilocular ovary and embryo with folded cotyledons. An investigation of the anther, female gametophyte, endosperm, and seed of *Picrodendron* and the Oldfieldioideae would be of considerable interest from a taxonomic viewpoint.

6. CALLITRICHACEAE

The euphorbiacean connection of the Callitrichaceae is indeed quite discredited (Webster, 1987a). The unitegmic, tenuinucellate ovules, differentiation of endothelium, cellular endosperm with terminal haustoria, long filamentous proembryonal suspensor, and minute seeds with membranous seed coats (Netolitzky, 1926; Maheshwari, 1963) are a far cry from the Euphorbiaceae. On the basis of their embryology and seed structure the Callitrichaceae are far more comfortable in or near the Lamiales (Stebbins, 1974; Takhtajan, 1980; Thorne, 1983; Dahlgren, 1983).

7. AEXTOXICACEAE

A monotypic family endemic to Chile, the Aextoxicaceae have been assigned to the Euphorbiales by Stebbins (1974), Takhtajan (1983), Thorne (1983), and Goldberg (1986); Hutchinson (1973), Cronquist (1981), Rouleau (1981), and Webster (1987a) prefer it to be in the Celastrales. This taxon is embryologically not well understood. It has

anatropous, bitegmic, crassinucellate ovules with massive nucellar beaks (Mauritzon, 1936). However, its bicarpellary, unilocular ovary with one bifid style and two subapical ovules (Goldberg, 1986), endostome extending considerably beyond the exostome, embryo extending only up to half the length of the endosperm, and ruminate endosperm give the impression that it may not be related to the Euphorbiaceae.

8. DICHAPETALACEAE

The Dichapetalaceae, a small family of four genera centered in Africa, have been included in the Euphorbiales (Emberger, 1960; Rouleau, 1981; Takhtajan, 1983; Thorne, 1983; Dahlgren, 1983), Rosales (Hutchinson, 1973), Thymelaeales (Melchior, 1964), and the Celastrales (Cronquist, 1981; Goldberg, 1986). Punt (1975) did not observe any significant resemblance of its pollen with that of the Euphorbiaceae and suggested its greater similarity with the Malpighiaceae. From what is known about its embryology, it seems that it has a bi- or tricarpellary ovary, two ovules in each locule on axile placentation, and carunculate seeds like those of the Euphorbiaceae. However, its unitegmic ovules (Corner, 1976) and exalbuminous seeds do not accord well with the Euphorbiaceae. Its resemblance is rather far more with the Icacinaceae (see Davis, 1966) and other Celastrales (Goldberg, 1986).

9. THYMELAEACEAE

The Thymelaeaceae have been placed in the Myrtales (Stebbins, 1974; Benson, 1979; Cronquist, 1981) and the Euphorbiales (Thorne, 1983). Takhtajan (1980) and Dahlgren (1983) raised them to an independent order, the Thymelaeales, which is juxtaposed to the Euphorbiales in the superorder Malviflorae.

Erdtman (1952) emphasized the resemblance in the "crotonoid" exine pattern of some Euphorbiaceae and Thymelaeaceae. Wunderlich (1967) and Corner (1976) pointed out that both these taxa are characterized by exotegmic seeds. Other common embryological features are: tetrasporangiate anther, fibrous endothecium, ephemeral middle layers, secretory tapetum, axile placentation, anatropous or hemianatropous, bitegmic crassinucellate ovules, presence of nucellar beak and hypostase, often carunculate seeds, and straight embryo extending all along the seed (see Davis, 1966; Corner, 1976). However, unlike Euphorbiaceae, the Thymelaeaceae have a stylar obturator and persistent and multiplicative antipodal cells, and the endosperm is usually scanty or absent. It is therefore better to assign the Thymelaeaceae to a separate order, the Thymelaeales, next to the Euphorbiales in the superorder Malviflorae. The alternative view of the alliance of the Thymelaeaceae with the Myrtales is much less convincing. The Myrtaceae have numerous ovules in the ovary, lack an obturator and hypostase, are frequently polyembryonous (Netolitzky, 1926; Corner, 1976) and have seeds that are ecarunculate, with a testal seed coat.

10. PANDACEAE

Pandaceae, another small family with four genera, is distributed mostly in western Africa and southeastern Asia. With their bilocular anthers, orthotropous ovules (in *Panda* Pierre), lack of obturator, and fruits dehiscing by valves (Goldberg, 1986), they no doubt deserve to be segregated from the Euphorbiaceae in an independent family, the Pandaceae. Whether this family should be placed in the Euphorbiales (Cronquist, 1981, 1988; Takhtajan, 1983, 1987; Thorne, 1983; Goldberg, 1986; Radcliffe-Smith, 1987) or allied to the Celastrales (Melchior, 1964; Hutchinson, 1973) cannot be stated unequivocally until more embryological data become available on the Pandaceae.

Affinities of the Euphorbiales

The Euphorbiales have been considered by different authors to be affiliated with one of the two subclasses, the Dilleniidae (Violales and Malvales) or the Rosidae (Celastrales and Geraniales). Suggestions with regard to the relationships of the Euphorbiales have been mostly confined to these four orders:

1. Celastrales (Stebbins, 1974; Cronquist, 1981, 1988);
2. Geraniales (Melchior, 1964; Webster, 1987a);
3. Violales (Hickey & Wolfe, 1975);
4. Malvales (Croizat, 1973; Takhtajan, 1980, 1987; Dahlgren, 1983; Thorne, 1983; Goldberg, 1986).

The Celastrales (which may include Aquifoliaceae, Stackhausiaceae, Icacinaceae, Siphonodontaceae, Sphenostemonaceae, and Goupiaceae, for purposes of the present comparison) are mostly trees and shrubs with bisexual flowers, tetrasporangiate anthers, 5- or 6-layered anther walls, fibrous endothecium, ephemeral middle layers, a secretory tapetum, a superior, semi-inferior or inferior ovary, two to five carpels, one to five (Celastraceae) or up to ten locules (Siphonodontaceae), mostly one or two ovules per locule (two to six in Siphono-

dontaceae and up to 18 per locule in Celastraceae), axile placentation, anatropous, bitegmic or unitegmic, crassinucellate or tenuinucellate ovules, a dorsal raphe in ovules with upwardly directed micropyle or ventral in ovules with downwardly directed micropyle, presence of endothelium, a *Polygonum* type of embryo sac, ephemeral antipodals, Solanad or Caryophyllad type of embryogeny, multiplicative testa with outer epidermis developing into a palisadelike layer, tegmen with outer epidermis forming thick-walled fibers, and capsular fruit (sometimes a drupe or berry).

The Celastrales differ from the Euphorbiales in having bisexual flowers, unitegmic, tenuinucellate ovules (in Aquifoliaceae), a dorsal raphe in ovules with micropyle facing upward, single-celled archesporium, 8–15 antipodal cells (in Stackhousiaceae), cellular endosperm (in Aquifoliaceae and Icacinaceae) with chalazal haustorium (Swamy & Ganapathy, 1957), Caryophyllad or Solanad type of embryogeny, embryo mostly small, and outer epidermis of outer integument forming a palisadelike layer. There are significant similarities, too, in the structure of anther, ovule, and in fibrous thickenings in the outer epidermis of the inner integument. The differences, however, far outweigh the similarities.

The Geraniales (including Geraniaceae, Oxalidaceae, Limnanthaceae, Tropaeolaceae, Viviani-aceae, and Balsaminaceae) are a cosmopolitan group, usually with herbs and shrubs. Their other characteristics are: bisexual flowers, 4- or 5-layered anther wall with secretory or amoeboid tapetum, three to five carpels, one, two, or several ovules per locule, axile placentation, anatropous, campylotropous or amphitropous, bitegmic, crassinucellate (Geraniaceae), unitegmic, tenuinucellate (Limnanthaceae) or bitegmic, tenuinucellate (Oxalidaceae) ovules. Endothelium, obturator, and hypostase are present. The female gametophyte is of the *Polygonum* type, the endosperm is nuclear or helobial, copious or absent, the embryo has haustorial proembryonal suspensor (Tropaeolaceae), and the embryogeny is of Solanad type. Seeds are sometimes arillate, and the exotegmen forms a mechanical layer with an undulated outline (Geraniaceae). The exotegmen is fibrous in Oxalidaceae, and seeds are unitegmic, pachychalazal in Balsaminaceae and Limnanthaceae (Davis, 1966; Johri, 1970; Narayana, 1970a–c; Corner, 1976).

The Geraniales exhibit considerable diversity among themselves. They differ from the Euphorbiales in many features, e.g., in the presence of amoeboid tapetum, several ovules in each locule, unitegmic and tenuinucellate ovules, endothelium, endosperm haustorium (in Limnanthaceae) and suspensor haustorium (in Tropaeolaceae), Solanad type of embryogeny, and artillate seeds. Although there is some resemblance in the fibrous or palisadelike exotegmen of the Oxalidaceae and Geraniaceae with the Euphorbiales, the behavior of the outer integument is quite different. The Geraniales are, therefore, unlikely to be close relatives of the Euphorbiales.

The Violales are a pantropical and subtropical group incorporating families such as the Flacourtiaceae, Passifloraceae, Caricaceae, Turneraceae, Violaceae, and Cucurbitaceae. They have tetrasporangiate anthers, a 5-layered anther wall, fibrous endothecium, secretory tapetum, three to five carpels, superior-inferior, usually monolocular ovary, mostly numerous ovules in each locule, parietal, rarely axile or apical placentation, anatropous, hemianatropous or orthotropous, bitegmic, crassinucellate ovules with nucellar cap, hypostase consisting of a pocket of cutinized cells (podium), tannin-containing postament and sclerotic chalazal part, *Polygonum* type of embryo sac, nuclear endosperm (often scanty or absent in seed), Asterad type of embryogeny, straight embryo with thin cotyledons, usually numerous seeds with aril arising from raphe, fibrous exotegmen, and fruit mostly a berry (Davis, 1966; D. Singh, 1970a–d; Kaur, 1970; Corner, 1976).

The Violales resemble the Euphorbiales in their structure of anther, ovule, and seed. However, certain characteristics of the violaceous families, such as their monolocular ovary, numerous ovules, parietal placentation, absence of obturator, persistent pollen tubes, Asterad type of embryogeny, aril arising from the raphe, and reduction or absence of endosperm, give the impression that they are widely separated from the Euphorbiaceae.

The Malvales, a cosmopolitan group of herbs, shrubs, and trees, predominantly distributed in the subtropical areas, include the Sterculiaceae, Elaeocarpaceae, Tiliaceae, Malvaceae, Dipterocarpaceae, and Bombacaceae. They have mostly bisexual flowers, bisporangiate or tetrasporangiate anthers, 4- or 5-layered anther wall, fibrous endothecium, ephemeral middle layers, secretory tapetum with multinucleate cells, polysiphonous pollen, usually five carpels, one to many ovules per locule, axile (rarely parietal) placentation, anatropous, hemianatropous or campylotropous, bitegmic, crassinucellate ovules, differentiated hypostase, multicellular archesporium, *Polygonum* type of embryo sac, ephemeral antipodal cells (rarely multiplicative), nuclear endosperm, sometimes with chalazal haustorium (Bombacaceae), Asterad

or Onagrad type of embryogeny, straight, curved or folded embryo, extending all along the length of the endosperm, winged, hairy or arillate seeds with exotegmen forming a palisadelike layer of sclerotic (Malpighian) cells, and capsule or schizocarpic fruit (Davis, 1966; Corner, 1976). Thus, the Malvales show abundant similarity with the Euphorbiales in the structure of the anther, ovule, embryo sac, endosperm, embryo, and seed, and are undoubtedly nearer to the Euphorbiales.

The relationship of the Euphorbiales with the major groups of dicotyledons is difficult to decide without some element of ambiguity because the groups in question are themselves rather ill-defined. Various taxonomists, such as Dahlgren (1975), Cronquist (1981, 1988), Thorne (1983), Takhtajan (1987), and Goldberg (1986) have composed their Celastrales, Geraniales, Violales, and Malvales in different ways and have placed them at varying distances from the Euphorbiales and from each other. Many of their smaller families are little known embryologically. At the present level of understanding, the Euphorbiales are undoubtedly closer to the Malvales than to the other three orders discussed here. In view of this, inclusion of the spurges among the Dilleniidae is justified on embryological grounds.

Classification of the Euphorbiaceae

The subfamilies of the Euphorbiaceae as circumscribed by Webster (1975, 1987a) can be characterized embryologically as follows:

SUBFAMILY 1. PHYLLANTHOIDEAE: 2-nucleate pollen grains with nonspinulose exine, two ovules per locule, dermal initiation of both integuments, well-developed nucellar beak, *Polygonum* type of embryo sac, broad cotyledons, ecarunculate seeds with fibrous exotegmen.

SUBFAMILY 2. OLDFIELDIOIDEAE: 2-nucleate pollen with usually spinulose exine, two ovules per locule, presence of nucellar cap, narrow cotyledons, often carunculate seeds (caruncle derived from inner epidermis of outer integument) with fibrous exotegmen.

SUBFAMILY 3. ACALYPHOIDEAE: 2-nucleate pollen, nonspinulose and noncrotonoid exine, one ovule per locule, subdermal initiation of both integuments, well-developed nucellar beak, monosporic or tetrasporic embryo sac (*Acalypha* and *Mallotus*), and carunculate seeds (caruncle derived from dermal as well as subdermal cells of outer integument) with palisadelike exotegmen.

SUBFAMILY 4. CROTONOIDEAE: 2- or 3-nucleate pollen mostly with "Croton" type of exine, one ovule per locule, subdermal initiation of both integuments, well-developed nucellar beak, presence of endosperm haustoria (in *Croton*) and hypocotyledonary seminal roots, mostly carunculate seeds with palisadelike exotegmen.

SUBFAMILY 5. EUPHORBIOIDEAE: 2- or 3-nucleate pollen with reticulate or tectate exine, one ovule per locule, subdermal initiation of both integuments, presence of nucellar beak or cap, monosporic or tetrasporic embryo sac (*Euphorbia* spp.), carunculate or ecarunculate seeds with palisadelike exotegmen.

On the basis of the distribution of the above-mentioned features, there is no doubt that the subfamilies and tribes of Euphorbiaceae share a large number of correlated characters. Even when they differ, usually a perceptible pattern of evolution is recognizable. As indicated by Webster & Rupert (1973) there is a definite trend of evolution of 3-nucleate pollen from a 2-nucleate condition within the Crotonoideae and Euphorbioideae. A nucellar beak is present in all the groups but there is a trend of reduction in the Phyllanthoideae, Oldfieldioideae, and Euphorbioideae. In *Euphorbia* some species have a nucellar beak, whereas others have only a cap. The female gametophyte is of the *Polygonum* type and only in Acalyphoideae and Euphorbioideae is there a localized derivation of tetrasporic embryo sac. Endosperm development is remarkably uniform, with initial free nuclear divisions and subsequent centripetal wall formation. *Croton* spp. are exceptional in having endosperm haustoria as well. The seeds are exotegmic and have developed a caruncle in correlation with the explosive mechanism of seed dispersal. In the Euphorbioideae, even when the caruncle is absent, the apical part of the outer integument proliferates to some extent, indicating a secondary loss. It is thus apparent that behind the façade of diversity, the Euphorbiaceae are in fact a homogeneous group that could have evolved on a monophyletic basis from an as yet unknown group within the Dilleniidae.

It is likely that the evolutionary line that gave rise to the Acalyphoideae, Crotonoideae, and Euphorbioideae split rather early from the line that produced the Phyllanthoideae (and Oldfieldioideae). This is inferred because the biovulate condition, the dermal initiation of both integuments, and the fibrous exotegmen in the Phyllanthoideae (and Oldfieldioideae ?) are fundamentally different from the uniovulate condition, the subdermal initiation of

both integuments, and the palisadelike exotegmen of the Acalyphoideae, Crotonoideae, and Euphorbioideae. Moreover, in the Oldfieldioideae the caruncle is reported to have a dermal origin (*Micrantheum*; Berg, 1975), whereas in the Acalyphoideae it is formed by the proliferation of both dermal and subdermal cells (*Chrozophora*; Bor & Kapil, 1976). In the Crotonoideae, too (*Codiaeum*; Bor & Bouman, 1974), the caruncle is constituted by the cells derived from dermal tissue of the outer integument. The Crotonoideae and Euphorbioideae seem to have evolved as independent lines from the Acalyphoideae (cf., Webster, 1987b).

Thus, the pattern of distribution of embryological characters in different subfamilies gives an impression that the evolution within the Euphorbiaceae has progressed as follows: (i) From an early ancestral condition one phyletic line gave rise to the Phyllanthoideae and the Oldfieldioideae; (ii) a second line gave rise to the Acalyphoideae from which the Crotonoideae and the Euphorbioideae evolved as separate lines.

Corner (1976) proposed a cleavage in the Euphorbiaceae on the basis of the fact that the Phyllanthoideae have fibrous exotegmen, whereas the Crotonoideae possess exotegmen with palisade (Malphighian) cells. According to him the palisadelike exotegmen of the Crotonoideae aligned them with the Bombacaceae–Malvaceae–Sterculiaceae–Tiliaceae. On the other hand, the fibrous exotegmen of the Phyllanthoideae made them look closer to the Celastraceae–Flacourtiaceae–Violaceae. In our opinion, the differences in seed structures do not indicate a diphyletic origin of the Euphorbiaceae, particularly because various intermediates are seen in the Euphorbiaceae family itself. For example, in *Bischofia* the exotegmen in the chalazal and micropylar parts is made up of palisadelike cells, whereas in the median regions it has fibers with ribbonlike thickenings.

Embryological data support the division of the family Euphorbiaceae into five subfamilies, as postulated by Webster (1975, 1987a). Since only 16 out of 50 tribes of the Euphorbiaceae are explored embryologically, it would be rather premature to give an opinion on tribal classification. Such an evaluation must await further work on the biology of reproduction of quite a large number of taxa.

Conclusions

A general survey of the embryological literature on the Euphorbiaceae gives an impression that it is an extensively investigated taxon. However, a critical appraisal leads us to conclude that our information is confined to only about 30 genera belonging to 16 tribes out of 300 genera and 50 tribes recognized by Webster. In spite of this lacuna, it is not preposterous to list out the embryological features that uniformly characterize this family. The Euphorbiaceae display a remarkable homogeneity in the structure and development of anther, microsporogenesis, placentation, ovule, endosperm, embryo, and seed. Variation in pollen nuclear number, integument initiation, extent of nucellar growth, development of the female gametophyte and caruncle seems to represent an understandable pattern of evolution.

Embryological evidence supports the treatment of the Euphorbiaceae as a monophyletic group. Among its suspected allies, the Dichapetalaceae, Aextoxicaceae, and Pandaceae are poorly studied, and what is known about them does not justify their inclusion in the Euphorbiales along with the Euphorbiaceae. Buxaceae, Callitrichaceae, Daphniphyllaceae, and Simmondsiaceae are better known embryologically but have hardly anything in common with the Euphorbiaceae. *Bischofia* and *Picrodendron* certainly deserve to be retained in the Euphorbiaceae on embryological grounds. The Euphorbiales appear to be closer to the Malvales and the Thymelaeales rather than to other orders, as has often been advocated by systematists.

On the basis of distribution of embryological characters, Webster's classification of Euphorbiaceae into five subfamilies is supported. It appears that the uniovulate Acalyphoideae separated rather early from the biovulate Phyllanthoideae (and Oldfieldioideae), the most primitive spurges. The Crotonoideae and the Euphorbioideae probably arose from the Acalyphoideae as distinct lines. Present limitations of embryological data prevent any comments on the tribal classification of this interesting group of plants.

Research on the embryology of the Euphorbiaceae holds considerable promise for further elucidation of the affinities and classification of this large family. Studies on some of the little known tribes, for example, those of the Oldfieldioideae, and interpretation of the data, together with information from other disciplines, would go a long way toward understanding the saga of the spurges.

Literature Cited

Airy Shaw, H. K. 1965. Diagnoses of new families, new names, etc., for the seventh edition of Willis's "Dictionary." Kew Bull. 18: 249–273.

———. 1966. Notes on the genus *Bischofia* Bl. (Bischofiaceae). Kew Bull. 21: 327–329.

BANERJI, I. 1949. A contribution to the life history of *Acalypha fallax* Muell. Arg. Bull. Bot. Soc. Bengal 3: 29–32.

——— & M. K. DUTT. 1944. The development of the female gametophyte in some members of the Euphorbiaceae. Proc. Indian Acad. Sci. Sec. B 20: 51–60.

BATTAGLIA, E. 1986. Embryological questions: 8. *Euphorbia dulcis* type versus *Fritillaria* type. Annali di Botanica (Roma) 44: 97–136.

BOUHARMONT, J. 1962. Fécondation de l'ovule et développement de la graine après croisement et autopollination chez *Hevea brasiliensis*. Cellule 62: 119–130.

BEER, T. & M. D. SWAINE. 1977. On the theory of explosively dispersed seeds. New Phytol. 78: 681–694.

BENSON, L. D. 1979. Plant Classification, 2nd ed. Heath, Lexington, Massachusetts.

BERG, R. Y. 1975. Fruit, seed, and myrmecochorus dispersal in *Micrantheum* (Euphorbiaceae). Norweg. J. Bot. 22: 173–194.

BHATNAGAR, A. K. 1978. Morphology and Embryology of some Taxa of Controversial Affinities. Ph.D. Thesis. Univ. of Delhi, India.

——— & MEENAKSHI GARG. 1977. Affinities of *Daphniphyllum*—Palynological approach. Phytomorphology 27: 92–97.

——— & R. N. KAPIL. 1973. *Bischofia javanica*—Its relationship with Euphorbiaceae. Phytomorphology 23: 264–267.

——— & ———. 1979. Ontogeny and taxonomic significance of anther in *Bischofia javanica*. Phytomorphology 29: 298–306.

——— & ———. 1982. Seed development in *Daphniphyllum himalayense* with a discussion on taxonomic position of Daphniphyllaceae. Phytomorphology 32: 66–81.

BOR, J. & F. BOUMAN. 1974. Development of ovule and integuments in *Euphorbia milii* and *Codiaeum variegatum*. Phytomorphology 24: 280–296.

——— & R. N. KAPIL. 1975. *Euphorbia geniculata*—Ovule to seed. Act Bot. Neerl. 24: 257–268.

——— & ———. 1976. Anatropy and ontogeny of the bitegmic ovule in *Chrozophora* A. H. L. Jussieu (Euphorbiaceae). Acta Bot. Neerl. 25: 385–400.

BOUMAN, F. 1974. Developmental Studies of the Ovule, Integuments and Seed in Some Angiosperms. Ph.D. Thesis. University of Amsterdam, The Netherlands.

BREWBAKER, J. L. 1967. The distribution and phylogenetic significance of binucleate and trinucleate pollen grains in the angiosperms. Amer. J. Bot. 54: 1069–1083.

CHOPRA, S. 1970. Development of female gametophytes in *Sapium sebiferum* Roxb. Curr. Sci. 39: 17–18.

——— & R. P. SINGH. 1969. Structure and development of seed in *Phyllanthus urinaria* L. J. Indian Bot. Soc. 48: 212–216.

CORNER, E. J. H. 1976. The Seeds of Dicotyledons, Vols. 1 & 2. Cambridge Univ. Press, Cambridge.

CROIZAT, L. 1973. Les Euphorbiacées vues en elles-mêmes, et dans leurs rapports envers l'angiospermie en général. Mem. Soc. Brot. 23: 5–206.

CRONQUIST, A. 1981. An Integrated System of Classification of Flowering Plants. Columbia Univ. Press, New York.

———. 1988. The Evolution and Classification of Flowering Plants, 2nd ed. The New York Botanical Garden, Bronx, New York.

DAHLGREN, R. 1975. A system of classification of the angiosperms to be used to demonstrate the distribution of characters. Bot. Not. 128: 119–147.

———. 1980. A revised system of classification of the angiosperms. Bot. J. Linn. Soc. 80: 91–124.

———. 1983. General aspects of angiosperm evolution and macrosystematics. Nordic J. Bot. 3: 119–149.

——— & A. E. VAN WYK. 1988. Structures and relationships of families endemic to or centered in southern Africa. Pp. 1–94 *in* P. Goldblatt & P. P. Lowry II (editors), Modern Systematic Studies in African Botany. Monogr. Syst. Bot. Missouri Bot. Gard. 25.

DANG-VAN-LIEM. 1962. Recherches sur l'Embryogène des Tricoques. Ph.D. Thèse. Université de Paris, Paris.

DAVIS, GWENDA L. 1966. Systemic Embryology of the Angiosperms. John Wiley & Sons, New York.

DUTT, M. K. 1942. Development of the microspores and the nuclear behaviour in the tapetal cells of *Putranjiva roxburghii*, Wall. Sci. & Cult. 8: 309–310.

EMBERGER, L. 1960. Traité de Botanique (Systématique), Tome II. Les Vegétaux Vasculaires. Masson, Paris.

ERDTMAN, G. 1952. Pollen Morphology and Plant Taxonomy: Angiosperms. Almqvist & Wiksell, Stockholm.

GALIMBERTI, Z. 1963. Embriologia di *Codiaeum variegatum* Blume var. *pictum* (Lodd.) Mull. Nuovo Giorn. Bot. Ital. 70: 21–32.

GOLDBERG, A. 1986. Classification, Evolution and Phylogeny of the Families of Dicotyledons. Smithsonian Institution Press, Washington.

HAKKI, H. I. 1985. Studies on West Indian plants 3. On floral morphology, anatomy, and relationship of *Picrodendron baccatum* (L.) Krug & Urban (Euphorbiaceae). Bot. Jahrb. Syst. 107: 379–394.

HAYDEN, W. J. 1977. Comparative anatomy and systematics of *Picrodendron*, genus incertae sedis. J. Arnold Arbor. 58: 257–279.

———, W. T. GILLIS, D. E. STONE, C. R. BROOME & G. L. WEBSTER. 1984. Systematics and palynology of *Picrodendron*: Further evidence for relationship with the Oldfieldioideae (Euphorbiaceae). J. Arnold Arbor. 65: 105–127.

HICKEY, L. J. & J. A. WOLFE. 1975. The bases of angiosperm phylogeny: Vegetative morphology. Ann. Missouri Bot. Gard. 62: 538–589.

HUTCHINSON, J. 1969. Tribalism in the family Euphorbiaceae. Amer. J. Bot. 56: 738–758.

———. 1973. The Families of Flowering Plants, 3rd ed. Clarendon Press, Oxford.

JOHRI, B. M. 1970. Limnanthaceae. Pp. 110–113 *in* Proc. Symposium on Comparative Embryology of Angiosperms. Indian National Science Academy, New Delhi.

——— & R. N. KAPIL. 1953. Contribution to the morphology and life history of *Acalypha indica* L. Phytomorphology 3: 137–151.

KAPIL, R. N. 1956a. Development of embryo sac and endosperm in *Chrozophora rottleri* A. Juss.: A reinvestigation. Bot. Gaz. 117: 242–257.

———. 1956b. A further contribution to the mor-

phology and life history of *Chrozophora* Neck. Phytomorphology 6: 278–288.
———. 1960. Embryology of *Acalypha* Linn. Phytomorphology 10: 174–184.
———. 1961. Some embryological aspects of *Euphorbia dulcis* L. Phytomorphology 11: 24–36.
——— & A. K. Bhatnagar. 1972. Endosperm in Euphorbiaceae—A critical appraisal. Pp. 376–393 *in* Y. S. Murty, B. M. Johri, H. Y. Mohan Ram & T. M. Verghese (editors), Advances in Plant Morphology. Rustogi Publishers, Meerut.
——— & ———. 1980. Embryology in relation to angiosperm taxonomy. Pp. 272–295 *in* P. K. K. Nair (editor), Glimpses in Plant Research, Vol. V. Vikas Publ. House, New Delhi.
——— & U. Kaul. 1972. Embryologically little known taxon—*Parrotiopsis jacquemontiana*. Phytomorphology 22: 234–245.
Kaul, U. & R. N. Kapil. 1974. *Exbucklandia opulnea*—From flower to fruit. Phytomorphology 24: 217–228.
Kaur, D. 1970. Turneraceae. Pp. 194–198 *in* Proc. Symposium on Comparative Embryology of Angiosperms. Indian National Science Academy, New Delhi.
Köhler, E. 1965. Die Pollenmorphologie der Biovulaten Euphorbiaceae und ihre Bedeutung für die Taxonomie. Grana Palynol. 6: 26–120.
Landes, M. 1946. Seed development in *Acalypha rhomboidea* and some other Euphorbiaceae. Amer. J. Bot. 33: 562–568.
Maheshwari, P. 1950. An Introduction to the Embryology of Angiosperms. McGraw-Hill, New York.
———. 1963. Embryology in relation to taxonomy. Pp. 55–97 *in* W. S. Turrill (editor), Vistas in Botany, Vol. IV. Pergamon Press, Oxford.
Mauritzon, J. 1936. Zur Embryologie der Berberidaceen. Acta Horti Gothob. 11: 1–18.
McCann, L. P. 1945. Embryology of the tung tree. J. Agric. Res. 71: 215–229.
Melchior, H. (editor). 1964. A. Engler's Syllabus der Pflanzenfamilien, Aufl. 12, Band II, Angiospermen, Gebrüder Borntraeger, Berlin.
Mennega, A. M. W. 1987. Wood anatomy of the Euphorbiaceae, in particular of the subfamily Phyllanthoideae. Bot. J. Linn. Soc. 94: 111 126.
Modilewski, J. 1911. Uber die abnormale Embryosackentwicklung bei *Euphorbia palustris* L. und andern Euphorbiaceen. Ber. Deutsch. Bot. Ges. 29: 430–436.
Mukherjee, P. K. 1957. Studies in the embryology of *Euphorbia hypericifolia* Linn. Bull. Bot. Soc. Univ. Saugar 9: 7–18.
———. 1958. The female gametophyte of *Acalypha malabarica* Muell. with a brief discussion on the Penaea type of embryo sac. J. Indian Bot. Soc. 37: 504–508.
———. 1962. Gametophytes of three Euphorbiaceae. Bull. Bot. Soc., Coll. Sci., Nagpur 3: 10–14.
———. 1964. Further contribution to the embryology of the genus *Acalypha* Linn. Proc. Natl. Acad. Sci. India, B. 34: 129–141.
———. 1965. Contribution to the embryology of *Euphorbia peltata* Roxb. Proc. Natl. Acad. Sci. India, B. 35: 327–337.
———. 1968. Trends of specialization in the family Euphorbiaceae. 1. Microsporangium and microsporogenesis. Maharashtra Vidnyan Mandir Patrika 3: 10–16.
——— & M. D. Padhye. 1964. Contribution to the embryology of the genus *Phyllanthus* Linn. Proc. Natl. Acad. Sci. India, B. 34: 117–128.
Muzik, T. J. 1954. Development of fruit, seed, embryo, and seedling of *Hevea brasiliensis*. Amer. J. Bot. 41: 39–43.
Nair, N. C. & V. Abraham. 1963. A contribution to the morphology and embryology of *Micrococca mercurialis* Benth. J. Indian Bot. Soc. 42: 583–593.
——— & ———. 1980. Floral morphology and embryology of *Tragia involucrata* L. var. *angustifolia* Hook. f. Pp. 95–101 *in* K. Periasamy (editor), Symposium on Histochemistry, Development and Structural Anatomy of Angiosperms. Autonomous P. G. Centre, University of Madras, Tiruchirapalli.
——— & M. Maitreyi. 1962. Morphology and embryology of *Sebastiania chamaelea*. Bot. Gaz. 124: 58–68.
Narayana, L. L. 1970a. Oxalidaceae. Pp. 114–116 *in* Proc. Symp. on Comparative Embryology of Angiosperms. Indian National Science Academy, New Delhi.
———. 1970b. Geraniaceae. Pp. 117–119 *in* Proc. Symp. on Comparative Embryology of Angiosperms. Indian National Science Academy, New Delhi.
———. 1970c. Balsaminaceae. Pp. 158–162 *in* Proc. Symp. on Comparative Embryology of Angiosperms. Indian National Science Academy, New Delhi.
Netolitzky, F. 1962. Anatomie der Angiospermen-Samen. P. 364 *in* K. Linsbauer (editor), Handbuch der Pflanzenanatomie, Bd. X. Gebrüder Borntraeger. Berlin.
Pal, A. 1972. Structure and development of seeds in *Croton oblongifolius* Roxb. P. 330 *in* Proc. 59th Indian Sci. Congr., Pt. III, Calcutta. [Abstract.]
Punt, W. 1962. Pollen morphology of the Euphorbiaceae with special reference to taxonomy. Wentia 7: 1–116.
———. 1975. Pollen morphology of the Dichapetalaceae with special reference to evolutionary trends and mutual relationships of pollen types. Rev. Palaeobot. Palynol. 19: 1–97.
Radcliffe-Smith, A. 1987. Segregate families from the Euphorbiaceae. Bot. J. Linn. Soc. 94: 47–66.
Raju, M. V. S. & A. N. Rao. 1953. The development of the male and female gametophytes in *Mallotus albus* Muell. J. Mysore Univ. 13: 5–8.
Rao, A. N. 1964. Notes on embryology of *Hevea brasiliensis*. Curr. Sci. 33: 739–740.
Rao, P. N. 1962. A note on the embryology of *Micrococca mercurialis* Benth. Curr. Sci. 31: 426–427.
———. 1970. Euphorbiaceae. Bull. Indian Nat. Sci. Acad. No. 41: 136–141.
——— & D. S. Rao. 1976. Embryology of cassava (*Manihot*). Proc. Indian Natl. Sci. Acad. B. 42: 111–121.
Rouleau, E. 1981. Guide to the Generic Names Appearing in the Index Kewensis and its Fifteen Supplements, IV: Conspectus Systematis. Cowansville, Quebec.
Sharma, K. D. 1955. Cyto-embryological studies in some Indian Euphorbiaceae. Sci. & Cult. 21: 270–271.
Singh, D. 1970a. Violaceae. Pp. 188–193 *in* Proc.

Symp. on Comparative Embryology of Angiosperms. Indian National Science Academy, New Delhi.

———. 1970b. Passifloraceae. Pp. 199–204 *in* Proc. Symp. on Comparative Embryology of Angiosperms. Indian National Science Academy, New Delhi.

———. 1970c. Caricaceae. Pp. 208–211 *in* Proc. Symp. on Comparative Embryology of Angiosperms. Indian National Science Academy, New Delhi.

———. 1970d. Cucurbitaceae. Pp. 212–219 *in* Proc. Symp. on Comparative Embryology of Angiosperms. Indian National Science Academy, New Delhi.

SINGH, R. P. 1954. Structure and development of seeds in Euphorbiaceae. *Ricinus communis* L. Phytomorphology 4: 118–123.

———. 1956. Development of endosperm and embryo in *Phyllanthus niruri* L. Agra Univ. J. Res. (Sci.) 5: 163–167.

———. 1965. Structure and development of seeds in *Codiaeum variegatum* Blume. J. Indian Bot. Soc. 44: 205–210.

———. 1968. Structure and development of seeds in Euphorbiaceae: *Melanthesa rhamnoides* Wt. Beitr. Biol. Pflanzen. 45: 127–133.

———. 1969. Structure and development of seeds in *Euphorbia helioscopia*. Bot. Mag. (Tokyo) 82: 287–293.

———. 1970a. Structure and development of seeds in *Putranjiva roxburghii* Wall. J. Indian Bot. Soc. 49: 99–105.

———. 1970b. Structure and development of seeds in Euphorbiaceae: *Jatropha* species. Beitr. Biol. Pflanzen. 47: 79–90.

———. 1972. Structure and development of seed in *Phyllanthus niruri* L. J. Indian Bot. Soc. 51: 73–77.

——— & S. CHOPRA. 1970. Structure and development of seeds in *Croton bonplandianum* Baill. Phytomorphology 20: 83–87.

——— & J. L. JAIN. 1965. Development of female gametophyte in *Euphorbia pilosa* L. Curr. Sci. 34: 611–612.

——— & A. PAL. 1968. Structure and development of seeds in Euphorbiaceae: *Dalechampia roezeliana* Muell.-Arg. Pp. 65–74 *in* Techn. Commun. Natl. Bot. Gard.

SINGH, V. & A. SINGH. 1975. Placentation in Euphorbiaceae. Ann. Bot. 39: 1137–1140.

STEBBINS, G. L. 1974. Flowering Plants: Evolution above the Species Level. Belknap Press of Harvard Univ. Press, Cambridge, Massachusetts.

SWAMY, B. G. L. & P. M. GANAPATHY. 1957. A new type of endosperm haustorium in *Nothapodytes foetida*. Phytomorphology 7: 331 336.

TAKHTAJAN, A. 1980. Outline of the classification of flowering plants (Magnoliophyta). Bot. Rev. 46: 225–359.

———. 1983. The systematic arrangement of dicotyledonous families. Pp. 180 201 *in* C. R. Metcalfe & L. Chalk (editors), 2nd ed., Vol. 2. Clarendon Press, Oxford.

———. 1987. Systema Magnoliophytorum. Institutum Botanicum Nomine V.L. Komarovii, Academia Scientiarum URSS, Leningrad.

TATEISHI, S. 1927. On the development of the embryo sac and fertilization of *Acalypha australis* L. Bot. Mag., Tokyo 41: 477–485.

THATHACHAR, T. 1952. Morphological studies in the Euphorbiaceae: I—*Acalypha lanceolata* Willd. Phytomorphology 2: 197–201.

———. 1953a. Morphological studies in the Euphorbiaceae. II. *Mallotus philippensis* M. Arg. Proc. Natl. Inst. Sci. India, B. 19: 469 474.

———. 1953b. Morphological studies in the Euphorbiaceae. J. Mysore Univ. 13B: 363–388.

THORNE, R. F. 1983. Proposed new realignments in the angiosperms. Nordic J. Bot. 3: 85 117.

VENKATESWARLU, J. & P. N. RAO. 1963. Endosperm in Euphorbiaceae and occurrence of endosperm haustoria in two species of *Croton* Linn. Curr. Sci. 32: 514–516.

———, ——— & D. S. RAO. 1973. Occurrence of stylar obturator in two Euphorbiaceae. Curr. Sci. 43: 128–129.

VENTURA, M. 1934. Sulla poliembrionia di *Mallotus japonicus* Muell. Arg. Ann. Bot. (Roma) 20: 568–578.

WAGENITZ, G. 1975. Flower reduction as central problem of angiosperm taxonomy. Bot. Jahrb. 96: 448–470.

WEBSTER, G. L. 1967. The genera of Euphorbiaceae in the southeastern United States. J. Arnold Arbor. 48: 303–430.

———. 1975. Conspectus of a new classification of the Euphorbiaceae. Taxon 24: 593–601.

———. 1987a. The saga of the spurges: A review of classification and relationships in the Euphorbiales. Bot. J. Linn. Soc. 94: 3–46.

———. 1987b. Evolution and distributional history of the Euphorbiaceae. P. 309 *in* XIV Int. Bot. Congress, Berlin. [Abstract.]

——— & E. A. RUPERT. 1973. Phylogenetic significance of pollen nuclear number in the Euphorbiaceae. Evolution 27: 524–531.

———, ——— & D. KOUTNIK. 1982. Systematic significance of pollen nuclear number in Euphorbiaceae, tribe Euphorbieae. Amer. J. Bot. 69: 407 415.

——— & B. D. WEBSTER. 1972. The morphology and relationships of *Dalechampia scandens* (Euphorbiaceae). Amer. J. Bot. 59: 573 586.

WIEHR, E. 1930. Beiträge zur Kenntnis der Anatomie der wichtigsten Euphorbiaceen Samen unter besonderer Berücksichtigung ihrer Erkennungsmerkmale in Futtermitteln. Landw. Versuchsstationen 110: 313 398.

WIGER, J. 1935. Embryological Studies on the Families Buxaceae, Meliaceae, Simarubaceae and Burseraceae. Ph.D. Thesis. Univ. of Lund, Lund.

WUNDERLICH, R. 1967. Some remarks on the taxonomic significance of the seed coat. Phytomorphology 17: 301–311.

LEGUMINLIKE PROTEINS AND THE SYSTEMATICS OF THE EUPHORBIACEAE[1]

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Abstract

Serological methods were used to elucidate legumin similarities, i.e., similarities between the major seed storage proteins present in the Euphorbiaceae and related families. The results support the separation of two rather than five subfamilies in the Euphorbiaceae. Extrafamiliar close relationships were detected with taxa from Violiflorae, Malviflorae (both subclass Dilleniidae), and Rutiflorae (subclass Rosidae). Therefore, maintaining these two subclasses as natural categories is not supported by the data reported here.

The Euphorbiaceae, comprised of approximately 8000 species and 300 genera, include a wide range of morphological diversity, such as broad-leaved trees from the tropical rainforest, succulents from arid ecosystems, annual weeds, and even a *Salvinia*-like water plant (*Phyllanthus fluitans* Benth.). Because of this great diversity, which includes substantial family characteristics (latex, number of seeds/carpels, basic chromosome numbers), the taxonomic position of the family continues to be in dispute (Webster, 1987). Are the Euphorbiaceae phyletically and taxonomically connected to orders included in the Dilleniidae (e.g., Dahlgren, 1983; Frohne & Jensen, 1992), the Rosidae (e.g., Ehrendorfer, 1991) or both (e.g., Baillon, 1858; Pax, 1924)? Although most authors consider the Euphorbiaceae to have arisen monophyletically, the strongly indicated separation into two (Dahlgren, 1980) or five (Webster, 1975, and 1994) subfamilies gives rise to speculation of di- or polyphyletic origin (Schultes, 1987).

The classification dilemma illustrates the need for additional taxonomic and phylogenetic criteria to improve our understanding of the systematics of this family. Molecular data obtained from the investigation of nucleic acids and proteins conducted for other taxonomic groups have proven to be valuable for such taxonomic research. In this investigation we utilized comparative data from legumin molecules, proteins that have been successfully included in the systematic research for similar projects (e.g., Jensen & Greven, 1984; Bergner & Jensen, 1989).

Leguminlike proteins are the major seed proteins in gymnosperms (Jensen & Berthold, 1989, for *Ginkgo*, and unpublished results for the conifers and Gnetatae) and angiosperms (Jensen & Büttner, 1981; Jensen & Grumpe, 1983; Jensen & Greven, 1984; Jensen, 1984; Bergner & Jensen, 1989; Fischer & Jensen, 1992). These proteins have proven to be important characters for the elucidation of phylogenetic relationships in similar investigations. Thus, a priori statements have been based on the omnipresence of leguminlike proteins in seed plants plus their relatively high variability in evolution. A posteriori statements have been supported by the evidence seed proteins, including legumin, have provided in a variety of systematic studies (Cristofolini, 1980; Fairbrothers et al., 1975; Fairbrothers, 1977, 1983; Jensen & Fairbrothers, 1983).

Methods and Materials

Immunogenic legumins were isolated from the seeds of *Phyllanthus calycinus* Labill. (Phyllanthoideae), *Ricinus communis* L. (Acalyphoideae), *Hevea brasiliensis* (Willd. ex A. Juss.) Müll. Arg., *Reutealis trisperma* (Blanco) A. Shaw (both Crotonoideae), and *Hura crepitans* L. (Euphorbioideae). Sources of the seeds are given in the Appendix. The purified proteins were injected into rabbits to elicit specific antisera ("reference systems"). These antisera and the antigens from about 30 Euphorbiaceae species and 100 non-Euphorbiaceae species were used in the subsequent two-

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dimensional immunodiffusion experiments on agar plates. The similarities and dissimilarities between the legumins from the different taxa were revealed qualitatively by spur-analysis of the precipitates (Lester et al., 1983). For details, see Vogel (1986).

Such data of relative similarity have proven to be relevant for systematic interpretation, because they separate qualitative units; quantitative measurements for the characterization of systematic similarities have proven useless when investigating multicharacter systems. The multicharacter systems used are represented by the reference antisera; each reference antiserum contains many kinds of antibodies specifically raised against the different determinants of the legumin molecule of one species. These different kinds of antibodies included in one monospecific antiserum are the "reference characters" in our systematic research.

Results

Intrafamiliar legumin affinities

For the five reference systems, i.e., *Phyllanthus calycinus*, *Ricinus communis*, *Hevea brasiliensis*, *Reutealis trisperma*, and *Hura crepitans*, the data from the mutual comparison of precipitates from all pairs of taxa used (i.e., A spurs B, B spurs A, A spurs B and B spurs A, A is identical with B) are listed in data matrices (Table 1a–e). Taxa in the data matrices are ranked according to the serological similarity in relation to the reference system.

For the systematic evaluation of the taxa included in this investigation, two criteria are especially important. (i) The relative position of serological similarity in relation to the reference taxon. This position is more or less given by the ranking in Table 1 and also by the simplified ranking groups shown in Figure 1. (ii) Identical serological reactivities of two cross-reacting taxa are important if their serological reactivity is close to the reactivity of the reference taxon. For example, the serological identity between *Andrachne colchica* Fisch. et Mey. ex Boiss. and *Securinega durissima* Gmel. is significant, since the high correspondence of both antigens to the reference system of *Phyllanthus calycinus* includes a large portion of their legumin molecule (Table 1a). In contrast, the identical reaction of *Jatropha curcas* L. and *Aleurites montana* (Lour.) Wilson cannot be used to postulate identical or highly similar legumins because their correspondence to the reference system only represents a very small part of their potential antigenic legumin reactivity (Table 1a).

The data are presented on the basis of a discrimination of the five subfamilies: Phyllanthoideae, Oldfieldioideae, Acalyphoideae, Crotonoideae, and Euphorbioideae, following Webster's classification (1975, 1994). No reference system from the Oldfieldioideae has been employed in this research.

Phyllanthoideae. Using *Phyllanthus calycinus* as a reference system (Table 1a and Fig. 1a), the other Phyllanthoideae genera *Reverchonia*, *Breynia*, *Andrachne*, *Securinega*, and—somewhat separated—*Margaritaria*, proved to be the most similar taxa (i.e., had the highest similarity indices). *Antidesma bunius* Spreng., another member of the Phyllanthoideae, is distantly connected. The reactions of all Crotonoideae and Acalyphoideae taxa did not exceed the outgroup reactivities; only for the Euphorbioideae *Homalanthus*, *Sapium*, and *Hura*, have relationships indicating affinities been observed.

Acalyphoideae. Chrozophora and *Mercurialis*, members of the subfamily Acalyphoideae, revealed the expected high similarity indices with the *Ricinus communis* reference system (Table 1b, and Fig. 1b). The similarity indices between *Ricinus* and the other two members of the Acalyphoideae, i.e., *Dalechampia* and especially *Mallotus*, are definitely lower. *Joannesia* (Crotonoideae) is high in similarity ranking and represents significant affinities between Crotonoideae and Acalyphoideae. *Hevea* (Crotonoideae), *Hura*, and *Homalanthus* (both Euphorbioideae) are serologically similar to each other. All Phyllanthoideae and Oldfieldioideae react in the range of Euphorbiaceae outgroups.

Crotonoideae. Two taxa revealed the highest similarity indices with the *Hevea brasiliensis* (Crotonoideae) reference system (Table 1c and Fig. 1c): *Manihot* (Crotonoideae) and *Ricinus* (Acalyphoideae). However, the serological similarities between both taxa and *Hevea* include different parts of the spectrum of serological reactivity. Next to these two genera, *Croton* (Crotonoideae), as well as *Homalanthus* and *Hura* (both Euphorbioideae), have more serological legumin characters in common with *Hevea* than the other Euphorbiaceae genera tested. The Phyllanthoideae and Oldfieldioideae genera produce low reactivity. The serological reactions of *Drypetes*, *Phyllanthus*, *Andrachne*, and *Securinega* (all Phyllanthoideae) with the *Hevea* antisystem were identical; the legumin precipitation of *Antidesma*, another member of the Phyllanthoideae, "spurs" the legumin precipitation of the four genera indicating a somewhat higher degree of similarity with *Hevea*.

Another reference system from the subfamily Crotonoideae, *Reutealis trisperma* (tribe Aleuri-

TABLE 1. Data matrices for the serological results from two 1-dimensional gel diffusion experiments using five reference systems, i.e., *Phyllanthus calycinus* Labill. (a), *Ricinus communis* L. (b), *Hevea brasiliensis* (Willd. ex A. Juss.) Müll. Arg. (c), *Reutealis trisperma* (Blanco) A. Shaw (d), *Hura crepitans* L. (e). | legumin of the left species spurs the upper species; – legumin of the upper species spurs the left species; + double spurring; ○ identical precipitation; ● blank. All generic names are spelled out in the Appendix.

The data are shown symmetrically. Boxes indicate taxa groups with identical or similar cross-reactivity. The interrupted line marks the maximum reactivity of the outgroups.

Right column: Similarity indices calculated according to the formula

$$S_i = \frac{S_c}{S_R} \times 100\ (\%)$$

$S = \Sigma| + \frac{1}{2}\Sigma+ + \frac{1}{2}\Sigma\bigcirc$ for each species, using the row data, where R = reference taxon and C = cross-reacting taxon.

a

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	S_i
Phyllanthus calycinus	1	●	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	100
Reverchonia arenaria	2	–	●	○	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	93
Breynia fruticosa	3	–	○	●	○	○	|	|	|	|	|	|		|	|		|										(81)
Andrachne colchica	4	–	–	○	●	○	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	87
Securinega durissima	5	–	–	○	○	●	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	87
H. populifolius	6	–	–	–	–	–	●	○	○	+	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	72
Sapium sebiferum	7	–	–	–	–	–	○	●	○	+	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	72
Hura crepitans	8	–	–	–	–	–	○	○	●	+	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	72
Margaritaria scandens	9	–	–	–	–	–	+	+	+	●	+		+	+	+	+	+	+	+								50
Omphalea trichotoma	10	–	–	–	–	–	–	–	–	+	●	+	+	+	+	|	+	|	|	|	|	|	|	|	|	|	52
Adelia ricinella	11	–	–	–	–	–	–	–	–		+	●	+	+	+	|	+	|	|	|	|	|	|	|	|	|	50
Ricinus communis	12	–	–		–	–	–	–	–	+	+	+	●	+	+	○	+	+	|	|	|	|	|	|	|	|	48
Manihot glaziovii	13	–	–	–	–	–	–	–	–	+	+	+	+	●	+	○	|	+	|	|	|	|	|	|	|	|	50
Hevea brasiliensis	14	–	–	–	–	–	–	–	–	+	+	+	+	+	●	○	+	+	|	|	|	|	|	|	|	|	48
Mercurialis annua	15	–	–		–	–	–	–	–	+	–	–	○	○	○	●	+	|	|	|	|	|	|	|	|	|	46
Antidesma bunius	16	–	–	–	–	–	–	–	–	+	+	+	+	–	+	+	●	+	|	|	|	|	|	|	|	|	46
Chrozophora tinctoria	17	–	–		–	–	–	–	–	+	–	–	+	+	+	–	+	●	○	○	○	|	|	|	|	|	35
S. fimbricalyx	18	–	–		–	–	–	–	–	+	–	–	–	–	–	–	–	○	●	○	○	○	○	|	|	|	22
Joannesia princeps	19	–	–		–	–	–	–	–	–	–	–	–	–	–	–	–	○	○	●	○	|	○	|	|	|	22
Mallotus tenuifolius	20	–	–		–	–	–	–	–	–	–	–	–	–	–	–	–	○	○	○	●	○	○	○	|	|	17
Euphorbia characias	21	–	–		–	–	–	–	–	–	–	–	–	–	–	–	–	–	○	–	○	●	–	○	○	|	15
Aleurites montana	22	–	–		–	–	–	–	–	–	–	–	–	–	–	–	–	–	○	○	○	–	●	○	○	○	11
Croton tiglium	23	–	–		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	○	○	○	●	○	○	9
Jatropha curcas	24	–	–		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	○	○	●	○	4

TABLE 1. *Continued.*

		b																														
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	S_i
Ricinus communis	1	●																														
Chrozophora tinctoria	2	−	●								+																					100
Mercurialis perennis	3	−	−	●							−																					95
Joannesia princeps	4	−	−	−	●					+	−	+		+		+		+														90
Hevea brasiliensis	5	−	−	−	−	●	+	+			+																					78
Hura crepitans	6	−	−	−	−	+	●	+	+		+			+																		81
H. populifolius	7	−	−	−	−	+	+	●	+	+	+																					78
Dalechampia scandens	8	−	−	−	−	−	+	+	●		+					+	+															78
Manihot esculenta	9	−	−	−	+	−	−	+	−	●	+		+																	+		72
Eremocarpus setigerus	10	−	+			+	+	+	+	+	●	+			+		+		+				+			+	+	+	+			72
Sapium sebiferum	11	−	−	−	+	−	−	−	−	−	+	●																				71
Jatropha curcas	12	−	−	−	−	−	−	−	−	+	−	−	●							+												69
Excoecaria bicolor	13	−	−	−	+	−	+	−	−	−	−	−	−	●			+															62
Euphorbia lathyris	14	−	−	−	−	−	−	−	−	−	+	−	−	−	●		+															60
Vernicia montana	15	−	−	−	+	−	−	−	+	−	−	−	−	−	−	●				+	+		+									55
Croton tiglium	16	−	−	−	−	−	−	−	+	−	+	−	−	+	−	−	●		+		+		+							+		50
Reutealis trisperma	17	−	−	−	+	−	−	−	−	−	−	−	−	−	+	−	−	●	+	+	+											48
Aleurites montana	18	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−	+	+	●	+	+						+	+				41
Baccaurea tetrandra	19	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	+	+	●									+			40
Andrachne colchica	20	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	+	+	+	−	●			+								41
Securinega suffruticosa	21	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−	●			+							40
Phyllanthus grandifolius	22	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−	+	−	−	−	−	−	●	+	+	+						31
Drypetes australasica	23	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	+	−	+	●	+		+	+		+		26
Micrantheum ericoides	24	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	+	●	+						22
Putranjiva roxburghii	25	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−	−	−	−	−	−	−	+	−	+	●	+	+				22
Bridelia tomentosa	26	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−	−	−	+	−	−	−	−	+	−	+	●					21
Glochidion glaucum	27	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−	−	−	+	−	−	−	−	+	−	+	−	●	+		+	14
Mallotus philippinensis	28	−	−	−	−	−	−	−	+	−	+	−	−	−	−	−	−	+	−	+	−	−	−	−	−	−	−	+	●		+	14
Antidesma bunius	29	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−	●		5
P. quadriloculare	30	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	+	−	●	3

TABLE 1. Continued.

		c																														
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	S_i
Hevea brasiliensis	1	●	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	100
Manihot esculenta	2	−	●	+	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	95
Ricinus communis	3	−	+	●	|	|	|	|	+	|	|	|	+	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	91
H. populifolius	4	−	−	−	●	+	+	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	86
Hura crepitans	5	−	−	−	+	●	+	|	|	|	|	|	|	+	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	84
Croton tiglium	6	−	−	−	+	+	●	|	+	|	+	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	81
Joannesia princeps	7	−	−	−	−	−	−	●	|	+	|	|	|	|	|	|	|	+	|	|	|	|	|	|	|	|	|	|	|	|	|	76
Chrozophora tinctoria	8	−	−	+	−	−	+	−	●	+	|	−	|	|	+	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	72
Sapium sebiferum	9	−	−	−	−	−	−	+	+	●	+	+	|	|	|	+	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	71
Reutealis trisperma	10	−	−	−	−	−	+	−	−	+	●	+	+	|	|	+	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	67
Euphorbia lathyris	11	−	−	−	−	−	−	−	|	+	+	●	+	+	|	|	|	|	+	|	|	|	+	|	|	|	|	|	|	|	|	|	66
Excoecaria bicolor	12	−	−	+	−	−	−	−	−	−	+	+	●	|	|	|	−	|	+	|	|	|	|	|	|	|	|	|	|	|	|	|	62
Jatropha curcas	13	−	−	−	−	+	−	−	−	−	−	+	−	●	|	|	+	|	+	|	|	|	|	|	|	|	|	|	|	|	|	|	59
Dalechampia scandens	14	−	−	−	−	−	−	−	+	−	−	−	−	−	●	|	|	|	|	|	+	|	|	|	|	|	|	|	|	|	|	|	55
Mercurialis perennis	15	−	−	−	−	−	−	−	−	+	+	−	−	−	−	●	|	−	|	|	|	|	|	|	|	|	|	|	|	|	|	|	52
Aleuritis montana	16	−	−	−	−	−	−	−	−	−	−	−	|	+	−	−	●	|	+	|	|	|	|	|	|	|	|	|	|	|	|	|	52
Mallotus philippinensis	17	−	−	−	−	−	−	+	−	−	−	−	−	−	−	|	−	●	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	50
Putranjiva roxburghii	18	−	−	−	−	−	−	−	−	−	−	+	+	+	−	−	+	−	●	+	+	−	|	|	|	|	|	|	|	|	|	|	|	|	41
Vernicia montana	19	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	●	|	|	+	+	|	|	|	|	|	|	|	|	|	|	36
Eremocarpus spec.	20	−	−	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−	+	−	●	|	|	|	|	|	|	|	|	|	|	|	|	|	38
Antidesma bunius	21	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	|	−	−	●	|	|	|	|	|	|	|	|	|	|	|	|	34
Drypetes australasica	22	−	−	−	−	−	+	−	−	−	−	+	−	−	−	−	−	−	−	+	−	−	●	○	○	○	|	|	|	|	|	|	|	|	28
Phyllanthus grandifolius	23	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	−	−	○	●	○	|	|	|	○	|	|	|	|	|	24
Andrachne colchica	24	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	○	○	●	○	|	|	○	|	|	|	|	|	21
Securinega suffrutic.	25	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	○	−	○	●	|	|	○	|	|	|	|	|	19
Baccaurea tetrandra	26	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	●	|	−	|	|	|	|	|	14
Glochidion glaucum	27	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	○	○	○	−	●	○	−	|	|	|	|	10
Bridelia tomentosa	28	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	○	●	|	|	|	|	|	9
Micrantheum ericoides	29	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	●	|	|	|	|	7
Petalostigma quadriloc.	30	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	●	|	|	|	0

TABLE 1. Continued.

		d																											
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	S_i
Reutealis trisperma	1	●	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	100
Vernicia montana	2	–	●	+	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	94
Aleurites montana	3	–	+	●	|	|	|	|	|	|	|	|	|	|	|	|	|	|	+	|	|	|	|	|	|	|	|	92
Jatropha curcas	4	–	–	–	●	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	88
D. scandens	5	–	–	–	–	●	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	85
Joannesia princeps	6	–	–	–	–	–	●	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	81
Croton tiglium	7	–	–	–	–	–	–	●	|	+	+	|	|	|	+	+	|	|	|	|	|	|	|	|	|	|	|	69
Euphorbia lathyris	8	–	–	–	–	–	–	–	●	+	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	71
Hura crepitans	9	–	–	–	–	–	–	+	+	●	|	–	–	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	65
Manihot esculenta	10	–	–	–	–	–	–	+	–	–	●	|	|	|	|	|	|	+	|	|	|	|	|	|	|	|	|	|	65
Excoecaria bicolor	11	–	–	–	–	–	–	–	–	|	–	●	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	65
M. philippinensis	12	–	–	–	–	–	–	–	–	|	–	–	●	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	62
Mercurialis perennis	13	–	–	–	–	–	–	–	–	–	–	–	–	●	|	+	|	|	|	|	+	|	|	|	|	|	|	|	50
Baccaurea tetrandra	14	–	–	–	–	–	–	–	–	–	–	–	–	–	●	|	|	|	|	|	|	|	|	|	|	|	|	|	50
Antidesma bunius	15	–	–	–	–	–	–	+	–	–	–	–	–	+	–	●	|	|	|	|	|	|	|	|	+	|	|	|	|	48
E. setigerus	16	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	●	|	–	|	|	|	|	|	|	|	|	|	|	40
Hevea brasiliensis	17	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	●	–	|	|	|	|	|	|	|	|	|	|	37
Andrachne colchica	18	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	●	|	|	–	|	|	|	|	|	|	|	38
Sapium sebiferum	19	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	●	+	|	|	|	+	|	|	|	|	29
H. populifolius	20	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	●	|	|	|	+	|	|	|	|	27
P. quadriloculare	21	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	|	–	–	●	|	|	|	|	|	|	|	29
Ricinus communis	22	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	●	+	|	|	|	|	|	17
Bridelia tomentosa	23	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	●	|	–	+	–	|	8
Glochidion glaucum	24	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	+	+	–	–	–	●	|	|	|	|	17
M. ericoides	25	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	●	|	|	|	12
P. grandifolius	26	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	●	|	|	6
S. suffruticosa	27	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	|	–	–	–	●	|	4

TABLE 1. Continued.

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	S_i
Hura crepitans	1	●	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	100
Ricinus communis	2	–	●	|	|	|	|	|	+	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	95
Excoecaria bicolor	3	–	–	●	○	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	91
H. populifolius	4	–	–	○	●	○	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	90
Sapium sebiferum	5	–	–	–	○	●	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	88
Joannesia princeps	6	–	–	–	–	–	●	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	83
Chrozophora tinctoria	7	–	–	–	–	–	–	●	|	–	–	|	–	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	69
Manihot esculenta	8	–	+	–	–	–	–	–	●	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	78
Jatropha curcas	9	–	–	–	–	–	–	|	–	●	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	76
Hevea brasiliensis	10	–	–	–	–	–	–	|	–	–	●	|	|	+	+	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	69
Mercurialis perennis	11	–	–	–	–	–	–	–	–	–	–	●	|	|	–	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	62
Reutealis trisperma	12	–	–	–	–	–	–	|	–	–	–	–	●	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	66
Croton tiglium	13	–	–	–	–	–	–	–	–	–	+	–	–	●	|	+	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	59
Euphorbia lathyris	14	–	–	–	–	–	–	–	–	–	+	|	–	–	●	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	60
Aleurites montana	15	–	–	–	–	–	–	–	–	–	–	–	–	+	–	●	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	53
Vernicia montana	16	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	●	|	+	|	|	|	+	|	|	|	+	|	|	|	|	|	|	|	|	|	|	43
Dalechampia scandens	17	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	●	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	45
Eremocarpus setigerus	18	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	●	|	|	|	+	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	41
Mallotus philippinensis	19	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	●	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	38
P. quadriloculare	20	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	●	|	–	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	31
Micrantheum ericoides	21	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	●	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	31
Securinega suffruticosa	22	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	+	–	–	–	–	●	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	33
Phyllanthus grandifolius	23	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	○	●	○	○	|	|	|	|	|	|	|	|	|	|	|	|	|	22
Andrachne colchica	24	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	○	●	○	|	|	|	|	|	|	|	|	|	|	|	|	|	21
Bridelia tomentosa	25	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	○	○	●	|	|	|	|	|	|	|	|	|	|	|	|	|	21
Antidesma bunius	26	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	●	○	○	○	|	|	|	|	|	|	|	|	|	10
Drypetes australasica	27	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	○	●	○	+	|	|	|	|	|	|	|	|	|	9
Putranjiva roxburghii	28	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	○	○	●	○	|	|	|	|	|	|	|	|	|	9
Baccaurea tetrandra	29	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	○	+	○	●	|	|	|	|	|	|	|	|	|	7
Glochidion glaucum	30	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	●	|	|	|	|	|	|	|	|	|	0

tideae), has been tested (Table 1d and Fig. 1d). Clearly the two other members of the tribe Aleuritideae, i.e., *Vernicia* and *Aleurites*, have proved to be the most similar taxa. The ranking of the other Crotonoideae genera was graded in the following decreasing order: *Jatropha–Joannesia–Croton–Hura–Manihot–Eremocarpus*. Again, the Phyllanthoideae showed the least legumin affinities; however, additional taxa were included in this group of low affinities: *Eremocarpus* (Crotonoideae) and especially taxa with strong serological connections with the *Hevea* reference system, i.e., *Hevea* (Crotonoideae), *Sapium*, *Homalanthus* (Euphorbioideae), and *Ricinus* (Acalyphoideae).

Euphorbioideae. The highest similarity indices with the *Hura crepitans* (Euphorbioideae) antisystem (Table 1e and Fig. 1e) have been observed for *Ricinus communis*, which is placed in the Acalyphoideae. The serologically identical genera *Excoecaria*, *Homalanthus*, and *Sapium* (all Euphorbioideae) follow. *Euphorbia* reveals affinities that are lower than most members of the Acalyphoideae and Crotonoideae. The similarity indices of the Phyllanthoideae and Oldfieldioideae are again the lowest and do not exceed the outgroup reactivities.

For a graphic representation of the data patterns and relationships between taxa, ordination techniques were preferred over cluster analyses. Cluster analyses like UPGMA or similar hierarchical methods lead to one-dimensional representations accompanied by a considerable loss of information compared to two- or three-dimensional ordinations. Also, the results of the reference experiments do not deliver a complete matrix of pairwise similarities, but they can be treated as five variables measuring identities in relation to the reference taxa. Such data are better analyzed by dimension reduction or ordination techniques than by cluster analyses. The resulting graphs simultaneously show similarities between all taxa and allow visual inspection of their relationships.

For the five reference taxa, the similarity values can be presented two-dimensionally with little deviation from the experimentally obtained data (Fig. 2). This graph clearly demonstrates close serological similarities between *Ricinus*, *Hura*, and *Hevea*, but a distant position for *Phyllanthus* is revealed.

Two scaling procedures, i.e., Principal Component Analysis (PCA) and Nonlinear Multidimensional Scaling (NMDS) (Rohlf, 1989) have been used to calculate multidimensional graphs for the five reference taxa plus the 13 genera that have been included in all five reference experiments (Fig. 3a, b). Since relative positions for the taxa included in both graphs (based on different, nonrelated statistical procedures) principally are identical, they adequately represent the relationships between the taxa. For the five reference taxa the relative positions are almost the same as shown in Figure 2.

With the additional taxa, the Phyllanthoideae are clearly separated from the Acalyphoideae + Crotonoideae + Euphorbioideae. Within the Phyllanthoideae, *Antidesma* is only distantly connected. This is also the case for *Mallotus* within the Acalyphoideae. When compared with other members of the Crotonoideae (e.g., *Hevea*), the Aleuritideae (*Aleurites*, *Reutealis*) are distantly located. *Euphorbia* is separated from the Hippomaneae (*Homalanthus*, *Sapium*) within the Euphorbioideae.

PCA has also been used for an ordination of a higher number of taxa, i.e., those that are included in at least four reference systems (Fig. 4). Although the separation of the Phyllanthoideae + Oldfieldioideae from the Acalyphoideae + Crotonoideae + Euphorbioideae becomes less distinct, a high similarity to Figure 3 can be observed. The resulting pattern again demonstrates the missing serological discrimination capacity between *Ricinus* (Acalyphoideae), *Hura* (Euphorbioideae), and *Hevea* (Crotonoideae) reference systems. On the contrary, the taxa connected to *Hevea* and *Reutealis* (both Crotonoideae) are clearly separated.

EXTRAFAMILIAR CONNECTIONS

For the elucidation of the major systematic connections between Euphorbiaceae and other angiospermous families, we investigated approximately 100 species from a large number of dicotyledonous plant families. These taxa were tested for the serological reaction of their leguminlike proteins with the antiserum against *Ricinus communis*. One to three species were used to represent each family tested.

Families with very low legumin similarity indices (= no or very weak serological reactions) were Asteraceae, Lauraceae, Pittosporaceae, and Ranunculaceae; families with low legumin similarity indices (= weak serological reactions) are shown in Table 2. Only the species of Table 3 revealed high legumin similarity indices, exceeding those of many Euphorbiaceae species (ranking graduated according to their relative serological reactivity with the *Ricinus communis* antisystem, with the Passifloraceae species as the most similar species; see tab. 9 in Vogel, 1986).

All taxa of high legumin similarity (Table 3) belong to the superorders Malviflorae, Rutiflorae, and Violiflorae. They are of interest in attempting

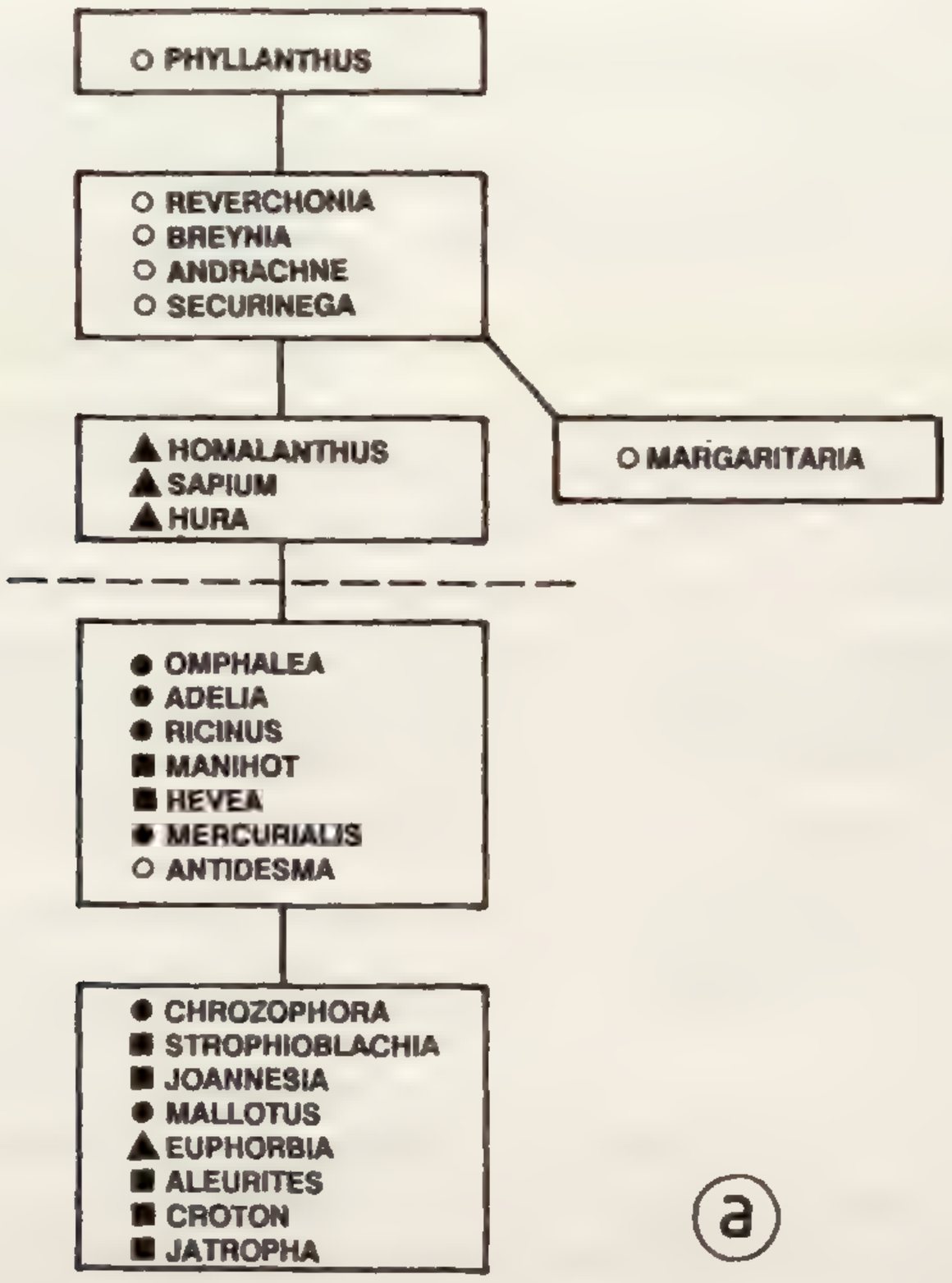

FIGURE 1. Simplified interpretation of the relative serological similarities in relation to each reference system, i.e., *Phyllanthus calycinus* (a), *Ricinus communis* (b), *Hevea brasiliensis* (c), *Reutealis trisperma* (d), *Hura crepitans*

(e). The interrupted line marks the maximum reactivity of the outgroups. Only generic names are used because of supposedly insignificant or undetectable serological infrageneric differences. ○ Phyllanthoideae; □ Oldfieldioideae; ● Acalyphoideae; ■ Crotonoideae; ▲ Euphorbioideae.

to interpret the relationships of the Euphorbiaceae to the other dicotyledons.

Species from the 11 families listed in Table 3 and another 18 families also belonging to the three superorders, plus one species each from the non-related Magnoliaceae, Scrophulariaceae, and Fabaceae were compared in a two-dimensional gel diffusion experiment using *Ricinus communis* as the reference antisystem. For a similar experiment using the *Phyllanthus calycinus* reference antisystem, only species from 11 top reacting families were included (except the Tropaeolaceae, since the protein material failed to react). The data matrix is given in Table 4. For all Malviflorae, Violiflorae, and Rutiflorae, the serological similarities are included in Figure 5.

Discussion

The Euphorbiaceae —One Family or Not?

The Phyllanthoideae (and Oldfieldioideae, which are only marginally considered in this investigation) differ in prominent characters from the other subfamilies, i.e., Acalyphoideae, Crotonoideae, and Euphorbioideae: the biovular locule (in contrast to the uniovular locule, characteristic for the other three subfamilies), the lack of latex and laticifers (which are present in almost all Acalyphoideae), and the basic chromosome number of 12 or 13 (Webster, 1975). The testa of the seeds are never developed in the form of palisades (Corner, 1976).

Although in most modern classifications the Phyllanthoideae are proposed to constitute a subfamily of the Euphorbiaceae, Huber (1985) proposed this taxon as a separate family that should be incorporated into the Linales. Bentham (1880) connected the Phyllanthoideae with the Rhamnales, with the exception of the "Hippomaneae," which he placed within the Urticales. Pax (1924) proposed a polyphyletic origin for the Euphorbiaceae, from both the Malvales and Geraniales.

Our serological results indicate that the legumins of the Phyllanthoideae are different from those of the Acalyphoideae, Crotonoideae, and Euphorbioideae (Fig. 3). In many cases (reference systems of *Hura* (Euphorbioideae), *Ricinus* (Acalyphoideae), *Hevea* (Crotonoideae)), the members of the Phyllanthoideae do not obviously exceed the affin-

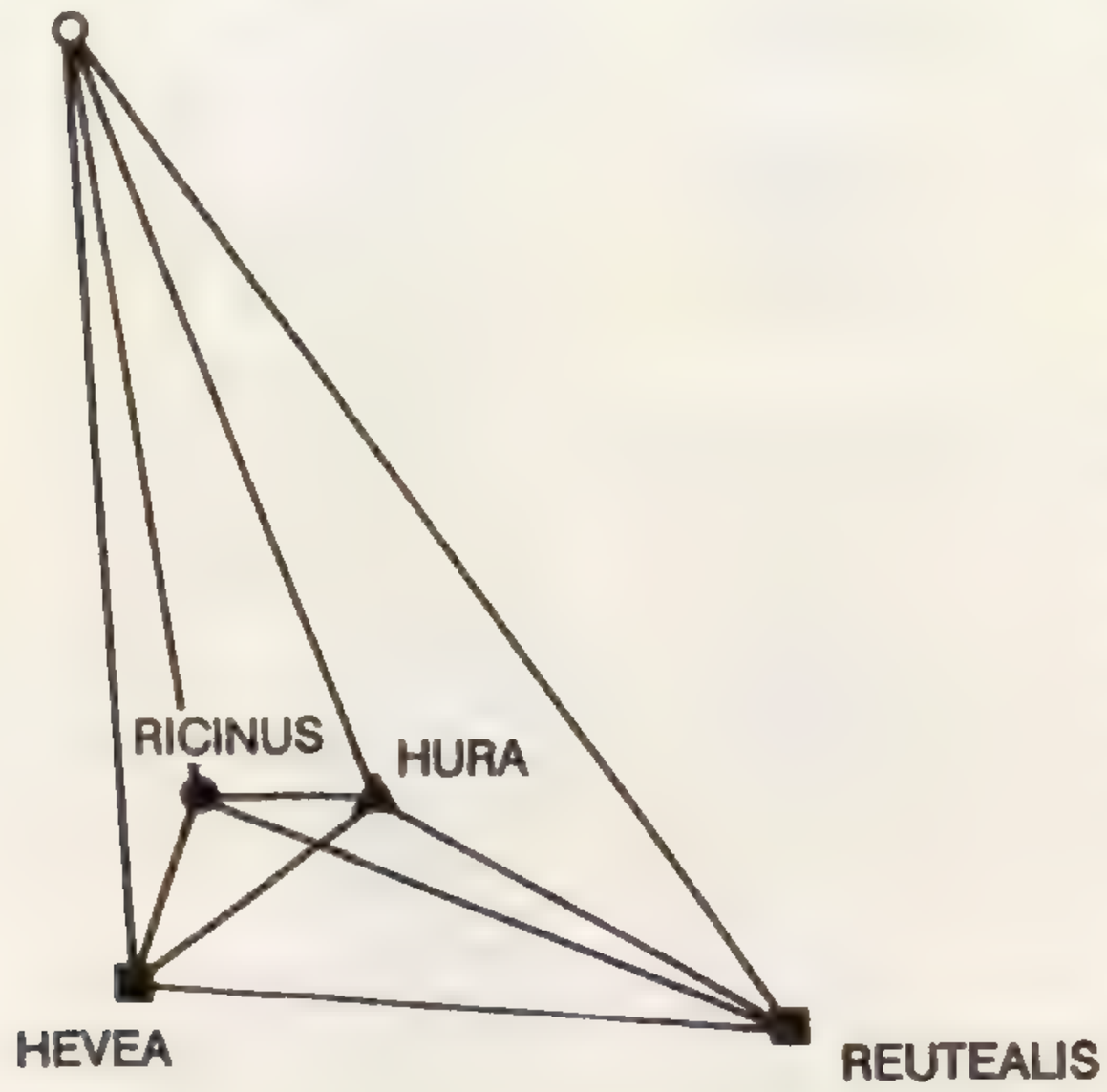

FIGURE 2. Graphic representation of serological distances (S.D.) for the five reference taxa *Phyllanthus*, *Hevea*, *Ricinus*, *Hura*, and *Reutealis*, calculated from the Similarity Indices of Table 1 (S.D. = 100 − S_i).

ities of the outgroups. However, in some cases our results indicate that the Phyllanthoideae are more closely related to the other three subfamilies than to the outgroup families: In the *Reuteales* (Crotonoideae) antisystem, the serological similarities of the Phyllanthoideae taxa *Baccaurea*, *Antidesma*, and *Andrachne* with *Reutealis* somewhat exceed the serological similarities of the outgroups with *Reutealis* (Fig. 1d). Similarly, in the *Phyllanthus* antisystem, the Euphorbioideae genera *Homalanthus*, *Sapium*, and *Hura* plus the Acalyphoideae genus *Omphalea* partly (i.e., by double spurring) exceed the outgroup reactions. Additionally, the reactivities of the outgroup antigens are very similar both with the antisystems of *Ricinus communis* and *Phyllanthus calycinus* (Table 4), and do not support proposals that suggest two different phylogenetic roots (Huber, 1985) for the Euphorbiaceae.

FIVE OR TWO SUBFAMILIES?

The serological data (Figs. 3 and 4) show that the legumins from *Ricinus communis* (Acalyphoideae), *Hevea brasiliensis* (Crotonoideae), and *Hura crepitans* (Euphorbioideae), i.e., from members of three different subfamilies, are remarkably similar. For the *Hura* (Euphorbioideae) reference system, *Ricinus communis* (Acalyphoideae) is the most similar cross-reacting species and is more closely connected than the other tested Euphorbioideae taxa from the genera *Excoecaria*, *Homalanthus*,

TABLE 2. Families, taxa of which show low legumin similarity indices with a *Ricinus communis* (Euphorbiaceae) antiserum. Classification is according to Dahlgren (1980).

Family	Order	Superorder
Araliaceae	Araliales	Araliiflorae
Berberidaceae	Ranunculales	Ranunculiflorae
Buxaceae	Buxales	Rosiflorae
Casuarinaceae	Casuarinales	Rosiflorae
Celastraceae	Celastrales	Santaliflorae
Combretaceae	Myrtales	Myrtiflorae
Daphniphyllaceae	Buxales	Rosiflorae
Fabaceae	Fabales	Fabiflorae
Fagaceae	Fagales	Rosiflorae
Gentianaceae	Gentianales	Gentianiflorae
Juglandaceae	Juglandales	Rosiflorae
Lythraceae	Myrtales	Myrtiflorae
Magnoliaceae	Magnoliales	Magnoliiflorae
Melastomataceae	Myrtales	Myrtiflorae
Myristicaceae	Annonales	Magnoliiflorae
Myrtaceae	Myrtales	Myrtiflorae
Onagraceae	Myrtales	Myrtiflorae
Papaveraceae	Papaverales	Ranunculiflorae
Primulaceae	Primulales	Primuliflorae
Proteaceae	Proteales	Proteiflorae
Rosaceae	Rosales	Rosiflorae
Saxifragaceae	Saxifragales	Rosiflorae
Scrophulariaceae	Scrophulariales	Lamiiflorae
Solanaceae	Solanales	Soianiflorae

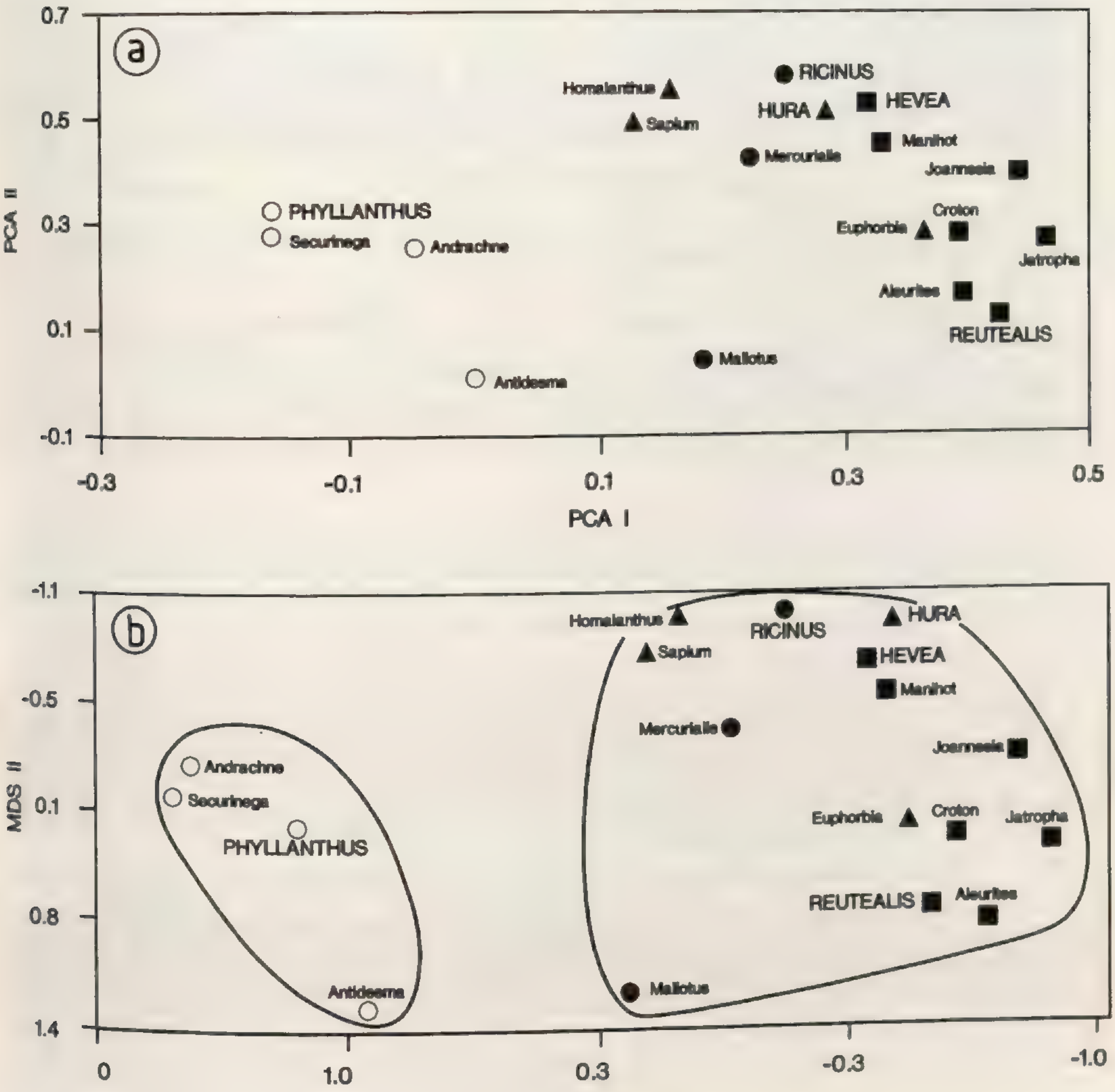

FIGURE 3. Two-dimensional ordinations of five variables equivalent to relative serological similarities between five reference taxa (capitals) and 13 nonreference taxa. For subfamily symbols see Figure 1.—a. PCA, two factors explaining 91% of variance.—b. MDS, based on pairwise average taxonomic distances (Sneath & Sokal, 1973), calculated from five variables. "Stress" = 0.095, indicating good conservation of the rank order of observed distances by the depicted interpoint distances, i.e., very good fit to observed distances.

Sapium, and *Euphorbia*. The correlation between the data of serological similarity from the three reference systems mentioned is high; the regression curve is about $y = x$ and almost identical for all correlation combinations (Vogel, 1986). This is not the case for the *Reutealis* reference system (Fig. 3), another reference system from the Crotonoideae, which indicated a considerable phylogenetic distance within the Crotonoideae in relation to the high correspondence obtained among the three subfamilies.

Thus the serological data do not support the separation of five subfamilies, but clearly indicate the separation of the Acalyphoideae–Crotonoideae–Euphorbioideae and the Phyllanthoideae as two phylogenetic groups. This conclusion is in agreement with the taxonomic treatments of several authors who designate the two subfamilies Phyllanthoideae and Hippomaneae (e.g., Dahlgren, 1980; Ehrendorfer, 1991).

SEROLOGICAL RELATIONSHIPS WITHIN THE SUBFAMILIES

Because the Oldfieldioideae have been margin-
ally compared, only data obtained for the Phyllan-

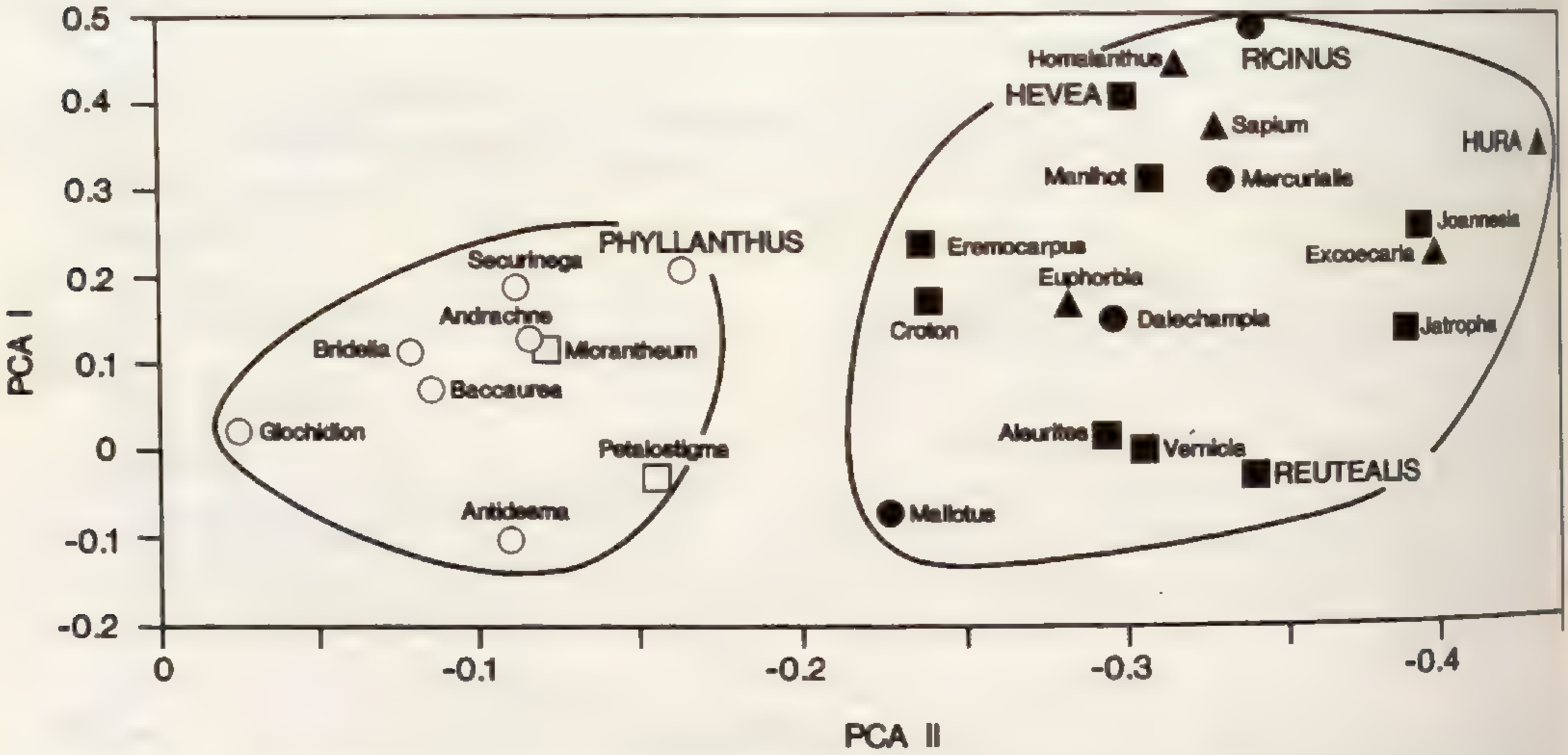

FIGURE 4. Two-dimensional ordinations of five variables equivalent to relative serological similarities between five reference taxa (capitals) and 22 nonreference taxa that have been incorporated in at least four reference experiments. PCA, two factors explaining 91% of variance. For subfamily symbols see Figure 1.

TABLE 3. Species with high legumin similarity indices with a *Ricinus communis* (Euphorbiaceae) antiserum. Classification is according to Dahlgren (1980).

Species	Family	Superorder
Adenia pechuelii	Passifloraceae	Violiflorae
Passiflora caerulea	—	
Hugonia orientalis	Linaceae	Rutiflorae
Linum usitatissimum	—	
Cneorum tricoccon	Cneoraceae	Rutiflorae
Tropaeolum majus	Tropaeolaceae	Rutiflorae
Daphne gnidium	Thymelaeaceae	Malviflorae
Daphne mezereum	—	
Pimelea ligustrina	—	
Antiaris africana	Moraceae	Malviflorae
Cudrania tricuspidata	—	
Morus rubra	—	
Celtis occidentalis	Ulmaceae	Malviflorae
Ulmus parvifolia	—	
Zelkova carpinifolia	—	
Dictamnus albus	Rutaceae	Rutiflorae
Phellodendron japonicum	—	
Ruta graveolens	—	
Zanthoxylum simulans	—	
Casearia gladiiformis	Flacourtiaceae	Violiflorae
Flacourtia inermis	—	
Idesia polycarpa	—	
Laportea moroides	Urticaceae	Malviflorae
Parietaria officinalis	—	
Urtica dioica	—	
Anacardium occidentale	Anacardiaceae	Rutiflorae
Toxicodendron verniciflua	—	
Spondias mombin	—	

TABLE 4. *Data matrix for the serological results from two-dimensional gel diffusion experiments, using three outgroup taxa and the reference systems* ***Ricinus communis*** (a) *and* ***Phyllanthus calycinus*** (b). *For further explanation see Table 1. The family ending "aceae" has been removed in some cases to allow for alignment of the table.*

		a																														
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	
Ricinus communis	1	●	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	Euphorbiaceae
Passiflora caerulea	2	−	●	|	|	|	|	+	+	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	Passifloraceae
Linum usitatissimum	3	−	−	●	|	|	|	|	|	|	|	+	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	Linaceae
Cneorum tricoccum	4	−	−	−	●	+	|	|	|	|	|	|	|	|	|	+	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	Cneoraceae
Tropaeolum majus	5	−	−	−	+	●	+	+	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	Tropaeolaceae
Daphne mezereum	6	−	−	−	−	+	●	|	+	|	|	|	|	|	+	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	Thymelae.
Morus rubra	7	−	+	−	−	+	−	●	|	+	|	|	|	|	+	|	+	|	|	+	+	|	|	|	|	|	|	|	|	|	|	|	Moraceae
Celtis occidentalis	8	−	+	−	−	−	+	−	●	+	+	|	+	+	+	|	|	|	+	|	|	+	|	|	|	|	|	|	|	|	|	|	|	Ulmaceae
Dictamnus albus	9	−	−	−	−	−	−	+	+	●	+	+	|	+	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	Rutaceae
Flacourtia inermis	10	−	−	−	−	−	−	−	+	+	●	+	|	+	|	|	|	+	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	Flacourtiaceae
Urtica dioica	11	−	−	+	−	−	−	−	−	+	+	●	|	+	+	+	|	|	+	|	+	|	|	|	|	|	|	|	|	|	|	|	|	|	Urticaceae
A. occidentale	12	−	−	−	−	−	−	−	+	−	−	−	●	+	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	Anacardiaceae
Magnolia tripetala	13	−	−	−	−	−	−	−	+	+	+	+	+	●	+	+	|	+	|	+	|	+	|	|	|	|	+	|	|	|	|	|	Magnoliaceae
Viola odorata	14	−	−	−	−	−	+	+	+	−	−	+	−	+	●	+	|	+	+	+	+	|	+	|	|	|	|	|	|	|	|	|	Violaceae
Hippophae rhamnoides	15	−	−	−	+	−	−	−	−	−	−	+	−	+	+	●	+	|	+	|	+	|	|	|	|	|	|	|	|	|	|	|	|	Elaeagnaceae
Sapindus saponaria	16	−	−	−	−	−	−	+	−	−	−	−	−	−	−	+	●	+	+	|	|	|	|	|	|	|	|	|	|	|	|	|	|	Sapindaceae
Cedrela odorata	17	−	−	−	−	−	−	−	−	−	+	−	−	+	+	−	+	●	+	+	+	|	+	+	+	|	|	|	|	|	|	|	Meliaceae
Digitalis purpurea	18	−	−	−	−	−	−	−	+	−	−	+	−	−	+	+	+	+	●	+	+	|	+	+	|	|	+	|	|	|	|	Scrophulari.
Terminalia catappa	19	−	−	−	−	−	−	+	−	−	−	−	−	+	+	−	−	+	+	●	+	|	+	|	|	|	|	|	|	|	|	Combretaceae
D. calycinum	20	−	−	−	−	−	−	+	−	−	−	+	−	−	+	+	−	+	+	+	●	|	+	+	+	+	+	|	|	|	|	Daphniphyll.
Lythrum salicaria	21	−	−	−	−	−	−	−	+	−	−	−	−	+	−	−	−	−	−	−	−	●	|	+	|	|	|	|	|	|		Lythraceae
Erodium botrys	22	−	−	−	−	−	−	−	−	−	−	−	−	−	+	−	−	+	+	+	+	−	●	+	+	|	+	|	|	|	|	Geraniaceae
Cucurbita maxima	23	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	+	−	+	+	+	●	+	+	|	|	|	|	|	Cucurbitaceae
Phaseolus vulgaris	24	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	−	−	+	−	+	+	●	+	|	|	|	|	|	Fabaceae
Cistus salviaefolius	25	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	−	−	+	+	●	|	|	|	|	|	Cistaceae
Celastrus scandens	26	−	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	+	−	+	−	+	−	−	−	●	|	+	|	|	Celastraceae
Impatiens balsamina	27	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	●	|	|	|	Balsaminaceae
Malva sylvestris	28	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	−	●	|	|	Malvaceae
Abroma augusta	29	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	●	|	Sterculiaceae
Rhamnus catharticus	30	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	●	Rhamnaceae

TABLE 4. Continued.

		b																			
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	
Phyllanthus calycinus	1	●	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	|	Euphorbiaceae
Linum usitatissimum	2	–	●	+	+	+	|	|	+	|	|	|	|	+	|	|	|	|	|	|	Linaceae
Pimelea ligustrina	3	–	+	●	+	+	+	+	|	|	|	|	|	|	|	+	+	|	|	|	|	Thymelaeaceae
Pteroceltis tatarinowii	4	–	+	+	●	○	|	+	|	+	|	|	|	|	|	|	|	|	|	|	|	Ulmaceae
Celtis occidentalis	5	–	+	+	○	●	+	+	|	+	+	|	○	|	|	|	|	|	|	|	|	|	Ulmaceae
Passiflora caerulea	6	–	–	+	–	+	●	+	+	+	|	|	|	|	|	|	|	|	|	|	|	|	Passifloraceae
F. cataphracta	7	–	–	+	+	+	+	●	+	+	+	+	+	+	+	|	|	|	|	|	|	|	Flacourtiaceae
Ficus carica	8	–	+	–	–	–	+	+	●	+	+	○	○	|	|	|	|	|	|	|	|	|	Moraceae
Cneorum tricoccon	9	–	–	–	+	+	+	+	+	●	○	+	+	+	○	|	|	|	|	|	|	|	Cneoraceae
C. pulverulentum	10	–	–	–	–	+	–	+	+	○	●	+	+	+	|	|	|	|	|	|	|	|	Cneoraceae
Daphne mezereum	11	–	–	–	–	–	–	+	○	+	+	●	○	+	+	○	|	|	|	|	|	|	|	Thymelaeaceae
Parietaria officinalis	12	–	–	–	–	○	–	+	○	+	+	○	●	○	+	+	|	|	○	|	|	|	|	Urticaceae
Urtica dioica	13	–	+	–	–	–	–	+	–	+	+	+	○	●	+	+	+	+	|	|	|	|	|	Urticaceae
Ptelea trifoliata	14	–	–	+	–	–	–	+	–	○	–	+	+	+	●	+	|	|	+	|	|	|	|	Rutaceae
Zanthoxylum alatum	15	–	–	+	–	–	–	–	–	–	–	○	+	+	+	●	○	|	|	|	|	|	|	Rutaceae
Citrus limon	16	–	–	–	–	–	–	–	–	–	–	–	–	+	–	○	●	+	|	|	|	|	|	Rutaceae
Hydnocarpus alpina	17	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	+	●	+	|	|	|	|	Flacourtiaceae
Laportea canadensis	18	–	–	–	–	–	–	–	–	–	–	–	○	–	+	–	–	+	●	+	|	|	|	Urticaceae
Toxicodendron vernicifluа	19	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	●	|	|	|	Anacardiaceae

thoideae, Acalyphoideae, Crotonoideae, and Euphorbioideae are discussed.

Phyllanthoideae. Reference genus: *Phyllanthus.*

Tested genera: *Bridelia* (tribe Bridelieae, according to Webster's treatment in this issue, 1994), *Antidesma, Baccaurea* (tribe Antidesmeae), *Drypetes, Putranjiva* (tribe Drypeteae), *Andrachne, Breynia, Glochidion, Margaritaria, Phyllanthus, Reverchonia, Securinega* (all tribe Phyllantheae).

Only seven genera included in the cross-reaction experiments with the *Phyllanthus* reference system (Fig. 1a) will be discussed. *Reverchonia, Breynia, Andrachne,* and *Securinega* are serologically the most similar genera to *Phyllanthus* among the tested taxa, in agreement with the inclusion of these four taxa within the tribe Phyllantheae. *Margaritaria* is less similar, and the double spurs with the precipitation of *Homalanthus, Sapium,* and *Hura* (Table 1a) can be interpreted in terms of overlapping similarity with *Phyllanthus. Antidesma* (tribe Antidesmeae) was found to be taxonomically and serologically different from the genera included in the Phyllantheae.

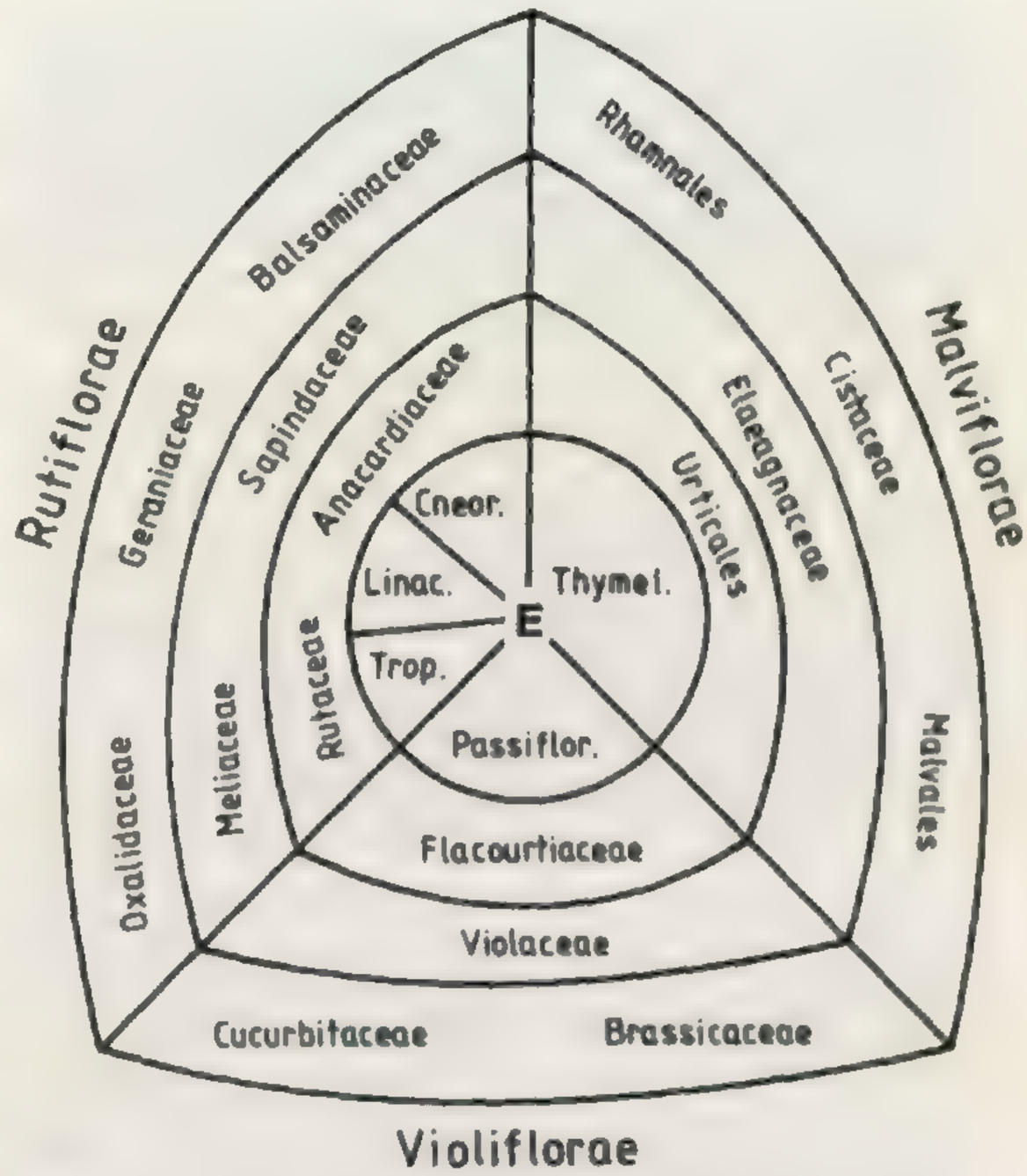

FIGURE 5. Serological similarities between the Euphorbiaceae (E) and outgroup families or orders of the Rutiflorae, Malviflorae, and Violiflorae. Similarity index decreases progressively from E toward the periphery.

Acalyphoideae. Reference genus: *Ricinus.*

Tested genera: *Chrozophora* (tribe Chrozophoreae), *Mallotus, Mercurialis, Ricinus* (all tribe Acalypheae), *Dalechampia* (tribe Plukenetieae), *Omphalea* (tribe Omphaleae), *Adelia* (tribe Adelieae).

The serological data (Table 1b, Fig. 1b) indicate close similarity between *Mercurialis* and *Ricinus* (both tribe Acalypheae). However, the affinities of *Chrozophora* (tribe Chrozophoreae) to *Ricinus* still exceed those of *Mercurialis.* The data reveal a strong legumin similarity between all three genera, which does not agree with the present tribal arrangements. Since the data from the *Hura* and *Hevea* reference systems also reveal decreasing affinities in the sequence *Ricinus–Chrozophora–Mercurialis,* the three genera should be phylogenetically connected to non-Acalyphoideae subfamilies through *Ricinus.*

Mallotus, although included in the tribe Acalypheae, demonstrates only a distant relationship to *Ricinus. Dalechampia* (tribe Plukenetieae) has a different legumin, which is in agreement with the separate tribal position. Both *Mallotus* and *Dalechampia* are connected with the *Reutealis* (Crotonoideae) reference system (Fig. 4).

Crotonoideae. Reference genera: *Hevea, Reutealis.*

Tested genera: *Hevea* (tribe Micrandreae), *Manihot* (tribe Manihoteae), *Jatropha, Joannesia* (both tribe Jatropheae), *Strophioblachia* (tribe Codieae), *Aleurites, Reutealis, Vernicia* (all tribe Aleuritideae), *Croton, Eremocarpus* (tribe Crotoneae).

The relationships of taxa included in the Crotonoideae were tested with two reference systems. They demonstrate a great phylogenetic complexity for this subfamily. From the comparison with the *Hevea* reference system (tribe Micrandreae) (Table 1c, Fig. 1c), the high serological correspondence with *Manihot* (tribe Manihoteae) and although of less degree—*Croton* (tribe Crotoneae) can be interpreted as supporting close relationships. However, the previous statement has to be kept in mind when interpreting the high serological correspondence with taxa from other subfamilies, i.e., *Ricinus* (Acalyphoideae), *Homalanthus* and *Hura* (both Euphorbioideae) The close relationship of *Jatropha* and *Joannesia* was not confirmed; *Jatropha* is loosely connected to the tribe Aleuritideae, whereas *Joannesia* is connected to *Hevea, Ricinus,* and *Hura* (Table 1c; Figs. 1c, 3). *Strophioblachia* (tribe Codieae) was employed in the experiments with the *Phyllanthus* reference system only, where it is close to *Joannesia.*

Aleurites, Reutealis, and *Vernicia* are all members of the tribe Aleuritideae subtribe Aleuritinae. They produce a similar legumin, which establishes their close relationship. The significance of this

statement is supported by the prominent cross-reactivities in the *Reutealis* reference system (Fig. 1d) and similar cross-reactivities in the other reference systems. The distant position of *Hevea* in this reference system is congruent with the concept of considerable phylogenetic differences between the Aleuritideae and the *Hevea–Hura–Ricinus* groups.

Euphorbioideae. Reference genus: *Hura.*

Tested genera: *Excoecaria, Homalanthus, Sapium* (all tribe Hippomaneae), *Hura* (tribe Hureae), *Euphorbia* (tribe Euphorbieae).

In this serological experiment *Excoecaria, Sapium,* and *Homalanthus* demonstrated structurally similar legumins, which support their inclusion in the same tribe Hippomaneae. They revealed close connections to *Hura* and also, especially in the case of *Homalanthus,* to the Crotonoideae genus *Hevea. Euphorbia* has no close serological affinities to either the Euphorbioideae reference system (*Hura*), nor to any other reference system used. Its major similarities are directed toward the *Reutealis* reference system. These reactions demonstrate the derived position of *Euphorbia* with respect to the molecular properties investigated, which is consistent with morphological characteristics.

RELATIONSHIPS BETWEEN EUPHORBIACEAE AND OTHER ANGIOSPERMS

Taxonomic and phylogenetic discussions on the relationships of the Euphorbiaceae within the angiosperms (see Webster, 1987) have suggested a common origin that favors the Malviflorae, Violiflorae, or Rutiflorae (Baillon, 1858; Bentham, 1878; Corner, 1976; Croizat, 1973; Dahlgren, 1983; Huber, 1985; Hutchinson, 1926; Lindley, 1836, 1853; Mueller, 1866; Pax, 1890, 1924; Takhtajan, 1969, 1980; Thorne, 1983; Webster, 1967; Wettstein, 1935). It is significant that data from our research, based upon the legumin properties, support the same systematic conclusions (see Table 3).

Although serological and morphological characters connect the Euphorbiaceae with Malviflorae, Violiflorae, or Rutiflorae, this does not apply to all taxa of the orders equally.

Malviflorae. Dahlgren (1980, 1983), Dahlgren et al. (1981), Takhtajan (1980), Thorne (1976, 1981), and many other authors regarded Euphorbiaceae and the order Malvales as related. The Rhamnales have been included in the discussions of relationship (Baillon, 1858; Bentham, 1878, 1880; Cronquist, 1981; Hutchinson, 1969; Lindley, 1853; Stebbins, 1974). However, neither the Malvales nor the Rhamnales have been found to be serologically related to the Euphorbiaceae. Therefore, we believe that phylogenetic relationships between Euphorbiaceae and Malvales, as well as between Euphorbiaceae and Rhamnales, are unlikely.

In contrast to the orders previously discussed, the Urticales (Moraceae, Urticaceae, Ulmaceae) prove to be serologically closely allied with the Euphorbiaceae. The serological characters in favor of these close phylogenetic relationships are supported by the following characters: reduced, often unisexual flowers and a hypogynous gynoecium containing a bitegmic and crassinucellate ovule in both the Euphorbiaceae and Urticales and the occurrence of laticifers in Euphorbiaceae and Moraceae. Additionally, chemical similarities (alkaloids, accumulation of calcium oxalate and silica) support the relationships between Euphorbiaceae and Urticales. Such evaluations have influenced Berg (1977), Dahlgren (1983), and Thorne (1976) to hypothesize close relationships between these two taxonomic groups.

The serological similarities between Euphorbiaceae and Urticales are exceeded by the similarities between Euphorbiaceae and Thymelaeaceae. Toxic phorbolic esters are produced in these two families (Frohne & Jensen, 1992). A crotonoid pollen exine and an exotegmic seed coat with a palisade layer derived from the outer epidermis of the inner integument (Wunderlich, 1968; Corner, 1976) are additional common characteristics. These characters confirm the close relationships between the two families. Several classifications included these families in the single order Euphorbiales to reflect this similarity (e.g., Frohne & Jensen, 1992; Thorne, 1968, 1983).

Violiflorae. Legumin antigens extracted from seeds of Cucurbitaceae and Brassicaceae species cross-reacted only weakly with Euphorbiaceae antisystems (references: *Phyllanthus* and *Ricinus*). However, members of the Violales, especially Flacourtiaceae and Passifloraceae, for which serological seed properties different from Cucurbitaceae have been reported by Kolbe & John (1979), share a relatively high portion of serological characters with the Euphorbiaceae. In cross-reactivity they exceed many Euphorbiaceae taxa. The flowers of Violales are characterized by, among other characters, three carpels, a hypogynous gynoecium, and bitegmic and crassinucellate ovaries. All these characters distinguish Euphorbiaceae flowers. Takhtajan (1969), Corner (1976), and Huber (1985) have regarded both groups as related. In this context the Flacourtiaceae have proven to be of interest because this family is regarded as es-

pecially closely connected to the phylogenetic origin of the Violales. Passifloraceae revealed the highest serological correspondence to the Euphorbiaceae reference systems of *Ricinus* (Table 4a) and also of *Phyllanthus* (Fig. 4b). A valvate calyx, starchless endosperm, straight embryo, and an extrastaminal floral disk are characteristic properties of the Passifloraceae, and these characters in addition to the seed protein data reinforce the theory of a close relationship between Violales and Euphorbiaceae.

Rutiflorae. Many Rutiflorae species included in our serological experiments revealed important positive cross-reactions. These cross-reactions demonstrated legumin similarities, with the Euphorbiaceae reference systems (*Phyllanthus* and *Ricinus*) being in the same range as the cross-reactions of many Euphorbiaceae species. However, the Balsaminaceae (Balsaminales), in contrast to the Linaceae (Geraniales), failed significantly to react as well as Oxalidaceae and Geraniaceae (both Geraniales). The following three Rutiflorae families revealed especially high legumin correspondence with the Euphorbiaceae: Tropaeolaceae, Cneoraceae, Linaceae.

The ovaries of the Tropaeolaceae fall apart into three coccae upon maturity, as do those of the Euphorbiaceae. They also possess an extrastaminate flower disk and stipulate leaves. Chemically, the production of glucosinolates is noteworthy because this is also reported for the Euphorbiaceae taxa *Putranjiva roxburghii* Wall. and *Jatropha multifida* L. (Rizk, 1987). In this connection it is important to recall that no serological similarities have been detected between the glucosinolate-producing Brassicaceae and the Tropaeolaceae (Jensen, 1991; Kolbe, 1978) or between Brassicaceae and Euphorbiaceae (Jensen, 1991).

For the Cneoraceae, the tricoccous gynoecium, floral disks, hypogynous ovaries, and one or two pendulous ovules per carpel are diagnostic characters. These important morphological similarities indicate possible close phylogenetic relationships between Cneoraceae and Euphorbiaceae; however, these characters have not been utilized in formulating classifications.

In the relative placement series of legumin similarities the Linaceae occupy the first (reference: *Phyllanthus*) or second placement (reference: *Ricinus*) among the families tested, and have been emphasized when the relationships of the Euphorbiaceae are discussed. In addition to serological characters, other characters indicate significant similarities between the Linaceae and Euphorbiaceae that cannot be explained by convergence alone. The Linaceae seeds produce copiously fatty oils and storage proteins, and are characterized by a hypogynous ovary, one or two bitegmic ovules for each carpel, an obturator, intra- or extrastaminal floral disks, and stipulate leaves.

ARE THE DILLENIIDAE AND ROSIDAE SUBCLASSES NATURAL GROUPS?

Our discussion of the relationships of the Euphorbiaceae indicates significant similarities between Euphorbiaceae and Malviflorae (especially Urticales and Thymelaeaceae), Violiflorae (especially Flacourtiaceae and Passifloraceae), and Rutiflorae (especially Tropaeolaceae, Cneoraceae, and Linaceae) (Fig. 5). The corresponding morphological similarities have been reported by several authors since Baillon's (1858) publication.

Thus the Euphorbiaceae are possibly closely related to the Dilleniidae (i.e., Malviflorae, Violiflorae) as well as to the Rosidae (i.e., Rutiflorae), which are two distinct subclasses in many classifications (e.g., Cronquist, 1981; Takhtajan, 1987). Therefore, the separation of the Dilleniidae and Rosidae subclasses has to be questioned and a taxonomic revision of the Dilleniidae–Rosidae-complex is considered necessary. Within this large collection of orders in the "Mittelbau" (Ehrendorfer, 1991) of the angiosperms, there is a group of families that show similar characters, i.e., stipulate leaves, reduced and sometimes unisexual flowers, floral disks, trimeric and hypogynous gynoecia with two or one ovules per carpel, bitegmic and crassinucellate ovules with obturator, laticifers, and cyanogenic and glucosinolate compounds. In this taxonomic complex, the Euphorbiaceae are included.

LITERATURE CITED

BAILLON, H. 1858. Etude Générale du Groupe des Euphorbiacées. Victor Masson, Paris.

BENTHAM, G. 1878. Notes on Euphorbiaceae. J. Linn. Soc., Bot. 17: 185–267.

———. 1880. Euphorbiaceae. *In:* G. Bentham & J. D. Hooker (editors), Genera Plantarum 3: 239–340.

BERG, C. C. 1977. Urticales, their differentiation and systematic position. Pl. Syst. Evol., Suppl. 1: 349–374.

BERGNER, I. & U. JENSEN. 1989. Phytoserological contribution to the systematic placement of the Typhales. Nordic J. Bot. 8: 447–456.

CORNER, E. J. H. 1976. The Seeds of Dicotyledons. 2 vols. Cambridge Univ. Press, Cambridge.

CRISTOFOLINI, G. 1980. Interpretation and analysis of serological data. Pp. 269–288 *in* F. A. Bisby, J. G. Vaughan & D. Wright (editors), Chemosystematics. Principles and Practice. Academic Press, London and New York.

CROIZAT, L. 1973. Les Euphorbiacées vues en elles-

mêmes, et dans leurs rapports envers l'angiospermie en général. Mem. Soc. Brot. 23: 5–206.

CRONQUIST, A. 1981. An Integrated System of Classification of Flowering Plants. Columbia Univ. Press, New York.

DAHLGREN, R. 1980. A revised system of classification of the angiosperms. Bot. J. Linn. Soc. 80: 91–124.

———. 1983. General aspects of angiosperm evolution and macrosystematics. Nordic J. Bot. 3: 119–149.

———, S. R. JENSEN & B. J. NIELSEN. 1981. A revised classification of the angiosperms with comments on correlations between chemical and other characters. Pp. 149–199 *in* D. A. Young & D. S. Seigler (editors), Phytochemistry and Angiosperm Phylogeny. Praeger, New York.

EHRENDORFER, F. 1991. Samenpflanzen. Pp. 699–828 *in* P. Sitte, H. Ziegler, F. Ehrendorfer & A. Bresinsky (editors), Lehrbuch der Botanik für Hochschulen. G. Fischer Verlag, Stuttgart, New York.

FAIRBROTHERS, D. E. 1977. Chemosystematics. Bull. Serol. Mus. 52: 3.

———. 1983. Evidence from nucleic acid and protein chemistry, in particular serology, in angiosperm classification. Nordic J. Bot. 3: 35–41.

———, T. J. MABRY, R. L. SCOGIN & B. L. TURNER. 1975. The bases of angiosperm phylogeny: Chemotaxonomy. Ann. Missouri Bot. Gard. 62: 765–800.

FISCHER, H. & U. JENSEN. 1992. Utilization of proteins to estimate relationships in plants: Serology. A discussion based on the Asteraceae–Cichorioideae. Belg. J. Bot. 125: 243–255.

FROHNE, D. & U. JENSEN. 1992. Systematik des Pflanzenreichs, 4. Aufl. G. Fischer Verlag, Stuttgart, New York.

HUBER, H. 1985. Angiospermen. Leitfaden durch die Ordnungen und Familien der Bedecktsamer. Gustav Fischer Verlag, Stuttgart, New York.

HUTCHINSON, J. 1926. The Families of Flowering Plants I. Dicotyledons. Macmillan, London.

———. 1969. Evolution and Phylogeny of Flowering Plants. Academic Press, London.

JENSEN, U. 1984. Legumin-like and vicilin-like storage proteins in *Nigella damascena* (Ranunculaceae) and six other dicotyledonous species. J. Pl. Physiol. 115: 161–170.

———. 1991. Steps toward the natural system of the dicotyledons: Serological characters. Aliso 13: 183–190.

——— & H. BERTHOLD. 1989. Legumin-like proteins in gymnosperms. Phytochemistry 28: 1389–1394.

——— & C. BÜTTNER. 1981. The distribution of storage proteins in Magnoliophytina (angiosperms) and their serological similarities. Taxon 30: 404–419.

——— & D. E. FAIRBROTHERS (editors). 1983. Proteins and Nucleic Acids in Plant Systematics. Springer-Verlag, Berlin, Heidelberg.

——— & B. GREVEN. 1984. Serological aspects and phylogenetic relationships of the Magnoliidae. Taxon 33: 563–577.

——— & B. GRUMPE. 1983. Seed storage proteins. Pp. 238–254 *in* U. Jensen & D. E. Fairbrothers (editors), Proteins and Nucleic Acids in Plant Systematics. Springer-Verlag, Berlin, Heidelberg.

KOLBE, K.-P. 1978. Serologischer Beitrag zur Systematik der Capparales. Bot. Jahrb. Syst. 99: 468–489.

——— & J. JOHN. 1979. Serologische Untersuchungen zur Systematik der Violales. Bot. Jahrb. Syst. 101: 3–15.

LESTER, R. N., P. A. ROBERTS & C. LESTER. 1983. Analysis of immunotaxonomic data obtained from spur identification and absorption techniques. Pp. 275–300 *in* U. Jensen & D. E. Fairbrothers (editors), Proteins and Nucleic Acids in Plant Systematics. Springer-Verlag, Berlin, Heidelberg.

LINDLEY, J. 1836. A Natural System of Botany. London.

———. 1853. The Vegetable Kingdom, 3rd ed. Bradbury & Evans, London.

MUELLER, J. 1866. Euphorbiaceae. *In:* A. P. de Candolle (editor), Prodromus Systematis Naturalis Regni Vegetabilis 15: 189–1261. Masson, Paris.

PAX, F. 1890. Euphorbiaceae. *In*: A. Engler & K. Prantl (editors), Die Natürlichen Pflanzenfamilien. Erste Auflage, III. 3: 1–119. W. Engelmann, Leipzig.

———. 1924. Die Phylogenie der Euphorbiaceae. Bot. Jahrb. Syst. 59: 129–182.

RIZK, A.-F. M. 1987. The chemical constituents and economic plants of the Euphorbiaceae. Pp. 293–326 *in* S. L. Jury, T. Reynolds, D. F. Cutler & F. J. Evans (editors), The Euphorbiales. Chemistry, Taxonomy and Economic Botany. Academic Press, London.

ROHLF, F. J. 1989. NTSYS-pc; Numerical Taxonomy and Multivariate Analysis System. Exeter Publishing, Setauket, New York.

SCHULTES, R. E. 1987. A new generic concept in the Euphorbiaceae. Bot. Mus. Leafl. 17: 27–36.

SNEATH, P. H. A. & R. R. SOKAL. 1973. Numerical Taxonomy. Freeman, San Francisco.

STEBBINS, G. L. 1974. Flowering Plants: Evolution Above the Species Level. Belknap Press, Harvard Univ., Cambridge, Massachusetts.

TAKHTAJAN, A. 1969. Flowering Plants, Origin and Dispersal. Oliver & Boyd, Edinburgh.

———. 1980. Outline of the classification of flowering plants (Magnoliophyta). Bot. Rev. Lancaster 46: 225–359.

———. 1987. Systema Magnoliophytorum. Nauka, Leninopoli. [In Russian.]

THORNE, R. F. 1968. Synopsis of a putatively phylogenetic classification of the flowering plants. Aliso 6: 57–66.

———. 1976. A phylogenetic classification of the Angiospermae. Evol. Biol. 9: 35–106.

———. 1981. Phytochemistry and angiosperm phylogeny: A summary statement. Pp. 233–295 *in* D. A. Young & D. S. Seigler (editors), Phytochemistry and Angiosperm Phylogeny. Praeger, New York.

———. 1983. Proposed new realignments in the angiosperms. Nordic J. Bot. 3: 85–117.

VOGEL, CH. 1986. Phytoserologische Untersuchungen zur Systematik der Euphorbiaceae. Dissertationes Botanicae, 98. J. Cramer, Berlin, Stuttgart.

WEBSTER, G. L. 1967. The genera of Euphorbiaceae in the south-eastern United States. J. Arnold Arbor. 48: 303–430.

———. 1975. Conspectus of a new classification of the Euphorbiaceae. Taxon 24: 593–601.

———. 1987. The saga of the spurges: A review of classification and relationships in the Euphorbiales.

Pp. 3–46 *in* S. L. Jury, T. Reynolds, D. F. Cutler & F. J. Evans (editors), The Euphorbiales: Chemistry, Taxonomy and Economic Botany. Academic Press, London.

———. 1994. Synopsis of the genera and suprageneric taxa of Euphorbiaceae. Ann. Missouri Bot. Gard. 81: 33–144.

WETTSTEIN, R. 1935. Handbuch der Systematischen Botanik. Vierte umgearbeitete Auflage. Deuticke, Leipzig.

WUNDERLICH, R. 1968. Some remarks on the taxonomic significance of the seed coat. Phytomorphology 17: 310–311.

APPENDIX. List of species used, with their sources.

Euphorbiaceae

Adelia ricinella L., seed stock Lehrstuhl Jensen
Aleurites montana (Lour.) Wils., Bot. Gard. Sri Lanka 1985
Andrachne colchica Fisch. et Mey. ex. Boiss., Bot. Gard. Wien 1984
Antidesma bunius (L.) Spreng., Bot. Gard. Salisburg 1977
Baccaurea tetrandra Muell. Arg., Bot. Gard. Basel
Breynia fruticosa (Muell. Arg.) Hook., seed stock Lehrstuhl Jensen
Bridelia tomentosa Bl., Bot. Gard. Wien
Chrozophora tinctoria (L.) A. Juss., Bot. Gard. Göttingen 1986
Croton tiglium L., Bot. Gard. Gießen 1984
Dalechampia scandens L., Bot. Gard. Basel
Drypetes australasica Pax & Hoffm., seed stock Lehrstuhl Jensen
Eremocarpus setigerus (Hook.) Benth., Bot. Gard. Honolulu
Euphorbia lathyris L., Bot. Gard. Rostock
Excoecaria bicolor Hassk., Bot. Gard. Basel
Glochidion glaucum Muell. Arg., Bot. Gard. Basel
Hevea brasiliensis (Willd. ex A. Juss.) Muell. Arg., Bot. Gard. Sri Lanka 1985
Homalanthus populifolius Grah., Bot. Gard. Wien 1984
Hura crepitans L., Bot. Gard. Sri Lanka 1985
Jatropha curcas L., Bot. Gard. Bogor 1984
Joannesia princeps Vell., Cutt. Lyon Arboretum, Honolulu
Mallotus philippinensis (Lam.) Muell. Arg., Bot. Gard. Bogor 1984
Manihot esculenta Crantz, Bot. Gard. Düsseldorf
Margaritaria discoidea (Baill.) Webster, Bot. Gard. Basel
Mercurialis perennis L., Bot. Gard. Basel
Micrantheum ericoides Desf., seed stock Lehrstuhl Jensen
Omphalea trichotoma Muell. Arg., seed stock Lehrstuhl Jensen
Petalostigma quadriloculare F. Muell., seed stock Lehrstuhl Jensen
Phyllanthus calycinus Labill., Bot. Gard. Basel
Putranjiva roxburghii Wall., Bot. Gard. Basel
Reutealis trisperma (Blanco) A. Shaw, Bot. Gard. Bogor 1984
Reverchonia arenaria A. Gray, coll. Webster Texas 1986
Ricinus communis L., Bot. Gard. Sri Lanka 1985
Sapium sebiferum (L.) Roxb., Bot. Gard. Siena 1983
Securinega durissima J. F. Gmel., Bot. Gard. Stuttgart-Hohenheim
Strophioblachia fimbricalyx Boerl., seed stock Lehrstuhl Jensen
Vernicia montana Lour., seed stock Lehrstuhl Jensen

Anacardiaceae

Anacardium occidentale L., Bot. Gard. Basel
Spondias mombin L., Bot. Gard. Wien 1984
Toxicodendron vernicifiua (Stokes) Barkl., Bot. Gard. Göttingen

Cneoraceae

Cneorum tricoccon L., Bot. Gard. Gießen

Flacourtiaceae

Casearia gladiiformis Mast., seed stock Lehrstuhl Jensen
Flacourtia inermis Roxb., Bot. Gard. Basel 1978
Idesia polycarpa Maxim., Bot. Gard. Wien 1988

Linaceae

Hugonia orientalis Engl., seed stock Lehrstuhl Jensen
Linum usitatissimum L., Reformhaus Sattran, Bayreuth

Moraceae

Antiaris africana Engl., seed stock Lehrstuhl Jensen
Cudrania tricuspidata (Carr.) Bur. ex Lavall., Bot. Gard. Wien 1988
Morus rubra L., Bot. Gard. Wien 1988

Passifloraceae

Adenia pechuelii (Engl.) Harms, seed stock Lehrstuhl Jensen
Passiflora caerulea L., Terra, Rosdorf

Rutaceae

Dictamnus albus L., seed stock Lehrstuhl Jensen
Phellodendron japonicum Maxim., Bot. Gard. Basel
Ruta graveolens L., seed stock Lehrstuhl Jensen
Zanthoxylum simulans Hance, seed stock Lehrstuhl Jensen

Thymelaeaceae

Daphne gnidium L., seed stock Lehrstuhl Jensen
Daphne mezereum L., seed stock Lehrstuhl Jensen
Pimelea ligustrina Labill., seed stock Lehrstuhl Jensen

Tropaeolaceae

Tropaeolum majus L., priv. Garden 1989

Ulmaceae

Celtis occidentalis L., seed stock Lehrstuhl Jensen
Ulmus parvifolia Jacq., Bot. Gard. Siena 1984
Zelkova carpinifolia (Pall.) K. Koch, seed stock Lehrstuhl Jensen

Urticaceae

Laportea moroides Wedd., Bot. Gard. Göttingen 1989
Parietaria officinalis L., Bot. Gard. Wien 1988
Urtica dioica L., Bot. Gard. Berlin-Dahlem 1984

SYSTEMATIC ANATOMY OF EUPHORBIACEAE SUBFAMILY OLDFIELDIOIDEAE.

W. John Hayden[2]

I. OVERVIEW[1]

Abstract

The biovulate subfamily Oldfieldioideae of Euphorbiaceae, characterized by spiny pollen, is an otherwise apparently diverse assemblage of mostly Southern Hemisphere trees and shrubs that traditionally have been allied with genera of Phyllanthoideae and Porantheroideae sensu Pax and Hoffmann. Although fairly diverse anatomically, the following structures characterize the subfamily with only a few exceptions: pinnate brochidodromous venation with generally randomly organized tertiary and higher order venation; foliar and petiolar glands absent; unicellular or unbranched uniseriate trichomes; latex absent; mucilaginous epidermis or hypodermis; brachyparacytic stomata; vessel elements with simple perforation plates and alternate, often very small, intervascular pits; thick-walled nonseptate imperforate tracheary elements; numerous narrow heterocellular rays; and abundant axial xylem parenchyma in diffuse to somewhat banded patterns and often bearing prismatic crystals. Anatomically, the shrubby Australian ericoid genera form a well-defined group with obvious affinities to the more arborescent Australasian genera, which show clear relationships to each other; the African and neotropical genera bearing compound leaves form another distinct group; the remaining genera are somewhat more isolated and seem to represent, in various cases, elements that are primitive within the subfamily or elements derived from the group bearing compound leaves. Presence of theoid teeth and palmately compound leaves in Oldfieldioideae are features consistent with Dilleniid origin for Euphorbiaceae.

As a taxonomic entity the euphorbiaceous subfamily Oldfieldioideae Köhler & Webster dates conceptually from the palynological studies of Punt (1962) and Köhler (1965) who noted the spiny pollen that characterizes the group; the assemblage recognized by pollen structure was subsequently formalized nomenclaturally as a new subfamily (Webster, 1967). In essence, pollen characters circumscribed a group of genera that previously had been assigned to the biovulate subfamilies Phyllanthoideae and Porantheroideae in the system of Pax & Hoffmann (1931). Webster's first (1975) classification of oldfieldioid genera contained several novel taxonomic associations at variance with earlier classifications, notably those of Pax & Hoffmann (1931) and Hutchinson (1969).

Interest in the anatomy of Oldfieldioideae stemmed from the need for comparative data to aid placement of the problematic genus *Picrodendron* Planchon (Hayden, 1977). Despite a number of publications dealing with the anatomy of oldfieldioid genera (Appendix 2), detailed information for most of the subfamily is lacking. Once *Picrodendron* was shown to be a member of Oldfieldioideae (Hayden, 1977; see also Hayden et al., 1984, and Hakki, 1985), an anatomical survey of the entire subfamily was initiated (Hayden, 1980) to assess relationships from data independent of reproductive (including pollen) morphology. Based in part on these anatomical studies, classification of Oldfieldioideae has been modified from Webster's (1975) original proposal; two broadly similar classifications, one by G. L. Webster (the preceding issue) and another by G. A. Levin and M. G. Simpson (this issue), are proposed elsewhere.

History

Classifications of Euphorbiaceae from the first half of the 19th century (e.g., Jussieu, 1824; Endlicher, 1836–1840) offer little insight into relationships among oldfieldioid genera. At this formative time in the definition of Euphorbiaceae (Webster, 1987) the few oldfieldioid genera known were often scattered widely in the family; moreover, some were referred to other families. Genera

[1] This study is based largely on a Ph.D. dissertation submitted to the University of Maryland, College Park. I thank W. L. Stern for assistance and guidance; H. K. Airy Shaw, L. J. Hickey, G. A. Levin, A. M. W. Mennega, and G. L. Webster were particularly helpful in providing specimens and/or comments; numerous others also provided specimens.

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of Pseudanthinae (or Caletieae in the traditional/narrow sense) were the first to be classified together, undoubtedly because of their shared ericoid xeromorphic habit and common provenance in Australia. Baillon (1858) grouped *Micrantheum* Desf. with *Pseudanthus* Sieber ex Sprengel, to which Agardh (1858) added *Stachystemon* Planchon, establishing the composition of Caletieae that was followed in all subsequent studies until the addition, first, of *Neoroepera* Muell. Arg. by Köhler (1965) and, now, the inclusion of all Australasian oldfieldioids as proposed by Levin & Simpson (1994, this issue) and Webster (1994). During the intervening years, however, the use of cotyledon width as the primary criterion for subdivision of the family (Mueller, 1866; Pax, 1890; Pax & Hoffmann, 1931) relegated the genera of Pseudanthinae (as Caletieae) to the Stenolobeae, a small group of Australian xerophytes with narrow cotyledons. Their somewhat isolated position in Stenolobeae minimized association of Pseudanthinae with other oldfieldioid genera.

Other oldfieldioid genera similarly suffered early taxonomic assignments that delayed consideration of relationships with the rest of the subfamily. Baillon (1858) submerged *Podocalyx* Klotzsch within the phyllanthoid genus *Richeria* Vahl, a disposition followed well into this century. *Oldfieldia* Benth. & Hook. f. was temporarily considered sapindaceous (Mueller, 1866; Baillon, 1878). Worse, the relationships of *Picrodendron* were long obscured by a series of misassignments at both the generic and familial levels (Hayden et al., 1984).

Aside from Caletieae sensu stricto, the genera of Oldfieldioideae were scattered widely in Mueller's (1866) treatment of the family for the *Prodromus*; *Mischodon* Thwaites was included with uniovulate genera, following an earlier error of Baillon (1858), *Oldfieldia* was still banished to Sapindaceae, and the remaining five oldfieldioid genera in his treatment were each assigned to different subtribes of Phyllantheae. Greater cohesiveness is apparent in a later publication of Baillon (1878). For example: *Choriceras* Baillon was included within Caletieae; *Austrobuxus* Miq. (as *Buraeavia* Baill.), *Longetia* Baillon ex Muell. Arg., *Petalostigma* F. Muell., and *Hyaenanche* Lambert formed a sequence; and *Dissiliaria* F. Muell. ex Baill. followed *Richeria* (which included the oldfieldioid *Podocalyx*). (See Webster (1987) for commentary on Baillon's peculiar "serial" system to indicate relationships.) Additional elements were gradually accreted to this loosely defined nucleus of oldfieldioid genera. Bentham (1880), in his treatment of Euphorbiaceae in the *Genera Plantarum*, included, using current nomenclature, *Dissiliaria*, *Longetia*, *Austrobuxus*, *Hyaenanche*, *Mischodon*, *Oldfieldia*, *Piranhea* Baillon, and only one nonoldfieldioid genus, *Bischofia* Blume, within genera 46–54. Although these plants constituted three discrete groups in his conspectus, Bentham (1878) expressed some doubt about their relatedness and he chose to associate *Neoroepera* and *Petalostigma* with other phyllanthoid genera. Pax (1890) treated oldfieldioid genera much as had Bentham; *Tetracoccus* Engelm. ex C. Parry, however, was included, and Pax & Hoffmann (1931) added *Petalostigma*, *Androstachys* Prain, and *Aristogeitonia* Prain to various subtribes consisting largely of oldfieldioid genera. Perhaps the first clear indication of the relatedness of oldfieldioid genera can be found in Pax's (1925) essay on Euphorbiaceae, which includes the phylogenetic tree reproduced in Figure 1. Although much of the detail in this phylogenetic tree may be challenged seriously in the light of present knowledge, it does show oldfieldioid genera (as usual, minus Pseudanthinae) comprising a clade distinct from other biovulate Euphorbiaceae.

In the disposition of genera, Hurusawa's (1954) classification of Euphorbiaceae essentially follows that of Pax & Hoffmann (1931) and thus contains no new insights on classification of oldfieldioid genera. In light of Pax's (1925) phylogeny and because of its disregard for the palynological data available at the time (Punt, 1962; Köhler, 1965), Hutchinson's (1969) classification was a retrograde development; oldfieldioid genera were widely distributed in five of 12 biovulate tribes, with three tribes mixing oldfieldioid and phyllanthoid elements. Hutchinson was the first, however, to associate *Paradrypetes* Kuhlm. with other oldfieldioid genera.

Airy Shaw (1965) entertained serious doubts about inclusion of several oldfieldioid genera in Euphorbiaceae. Accordingly, he proposed Androstachydaceae, of uncertain relationships, to accommodate *Androstachys*; he recognized Picrodendraceae as distinct from but allied to Euphorbiaceae; and he viewed *Aristogeitonia*, *Calaenodendron* Standley, *Mischodon*, *Oldfieldia*, and *Piranhea* as occupying an intermediate position between these families (Airy Shaw, 1966, 1972, 1973). Airy Shaw (1983) continued to accept an isolated taxonomic position for Stenolobeae (including Pseudanthinae), but he did, consistently, group the remaining Australasian genera of Oldfieldioideae in adjacent tribes in several of his informal or tentative classification systems (e.g., Airy Shaw, 1975, 1980b, 1983).

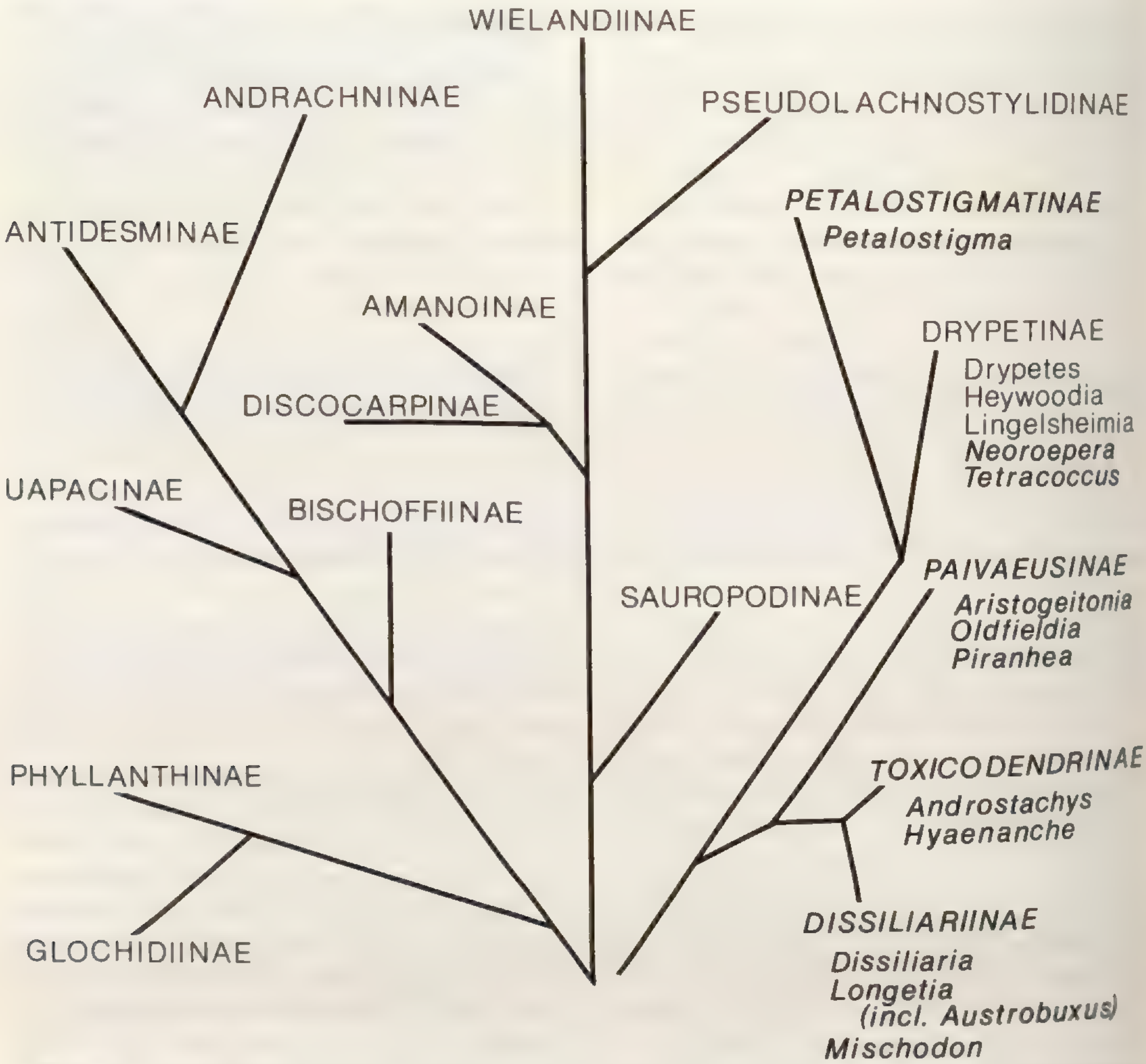


FIGURE 1. Relationships of subtribes of Phyllantheae, after Pax (1925). Right-hand clade is the earliest published phylogram of Oldfieldioideae. Generic composition of subtribes, where indicated, follows Pax & Hoffmann (1931); oldfieldioid taxa are in bold italics. Other than Pseudantheae, *Podocalyx* (treated as a subgenus of *Richeria* [Antidesminae]) is the only element of Oldfieldioideae known to Pax and not included in the phylogram.

DESCRIPTION, CIRCUMSCRIPTION, AND DISTRIBUTION

Plants of Oldfieldioideae are woody, ranging from low depressed shrubs to tall trees. Latex is absent and vestiture consists of unicellular or uniseriate trichomes. Leaves are alternate, opposite, or whorled and may be simple or palmately compound; petiolar and laminar glands are absent; stipules may be present or absent. Leaves may be strongly reduced in xerophytic species. Plants are typically dioecious. Flowers are apetalous, and most lack discs. Stamens range from three to many. Pollen is binucleate, with four to many brevicolporate to porate apertures; the exine lacks a foot layer, bears a discontinuous interstitium and thick perforate tectum with prominent supratectal spines (Levin & Simpson, 1994, this volume). Gynoecia consist of two to five carpels; styles are generally undivided; each locule houses a pair of pendulous anatropous ovules. Seeds are often carunculate and usually possess copious endosperm. Reports of $n = 12$ for *Pseudanthus* (Hassall, 1976), $2n = 48$ for *Picrodendron* (Fritsch, 1972), $n = 24$ for *Mischodon* and *Tetracoccus* (Hans, 1973), and $n = 24$, $2n = 48$ for *Mischodon* (Sarkar & Datta, 1980) collectively suggest a base number of $x = 12$ for the subfamily.

The first comprehensive classification of Oldfieldioideae (Webster, 1975) included 21 genera, but several changes in composition have occurred since then. Two newly discovered genera, *Voatamalo* Capuron ex Bosser (1976) and *Whyanbeelia* Airy Shaw & B. Hyland (Airy Shaw, 1976), have

been referred to the subfamily. Two enigmatic genera, *Croizatia* Steyerm. (Webster et al., 1987) and *Paradrypetes* (Levin, 1992), have been assigned to Oldfieldioideae following discovery of diagnostic flowering material and, especially, after study of pollen from these plants. *Kairothamnus* Airy Shaw (1980a) and *Scagea* McPherson (1985) have been segregated from *Austrobuxus* sensu lato, as has *Canaca* Guillaumin, if only tentatively (Webster, 1994). In recent years Radcliffe-Smith has redefined generic limits for several Oldfieldioideae. He has included *Paragelonium* Léandri within *Aristogeitonia* (Radcliffe-Smith, 1988), he segregated *Stachyandra* R.-Sm. from *Androstachys* to accommodate several Madagascan species bearing compound leaves (Radcliffe-Smith, 1990), and he expanded *Pseudanthus* to include *Stachystemon* (Radcliffe-Smith, 1993). The number of genera now stands at 27. (Solely because of the recency of its reclassification, *Stachystemon* is herein treated as a distinct genus.)

Genera of Oldfieldioideae are mostly mono- or oligotypic. *Austrobuxus*, with perhaps 20 species, is the most speciose, followed by *Pseudanthus* (seven species) and *Petalostigma* (six species). The total number of species referable to the subfamily is estimated at 86, approximately 1 percent of the total number of species in Euphorbiaceae.

Oldfieldioideae is largely a southern hemisphere group. Only three genera occur in areas not derived from the breakup of Gondwanaland; these are *Celaenodendron*, from western Mexico, *Picrodendron*, from the Bahamas and Greater Antilles, and *Tetracoccus* from Mexico and the southwest United States. Eight genera and 16 species occur in the New World, six genera and 16 species occur in Africa and Madagascar, one monotypic genus occurs in southern India and Sri Lanka, and 13 genera and 52 species are Australasian. No genus of Oldfieldioideae has a bicontinental distribution, although *Androstachys* and *Aristogeitonia* occur both in Madagascar and Africa.

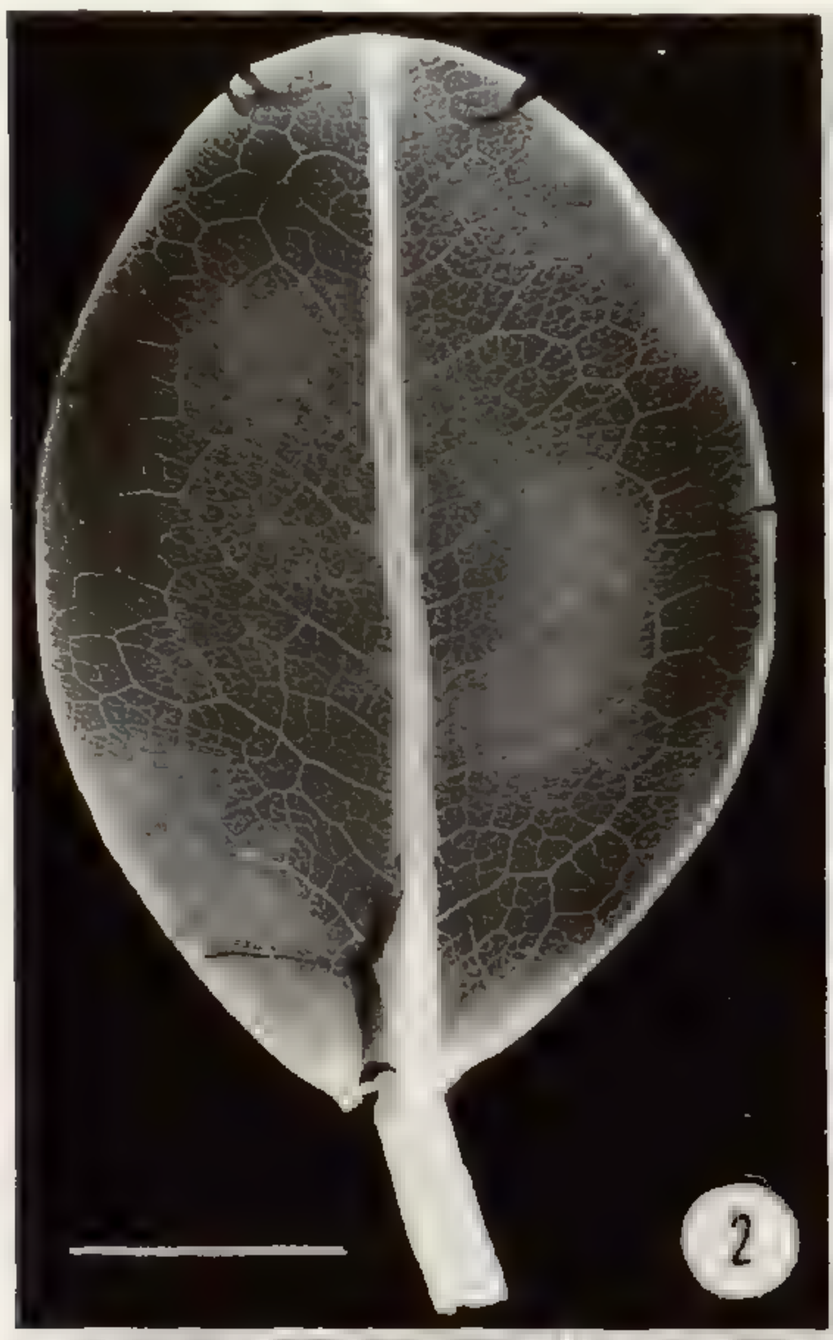
Materials

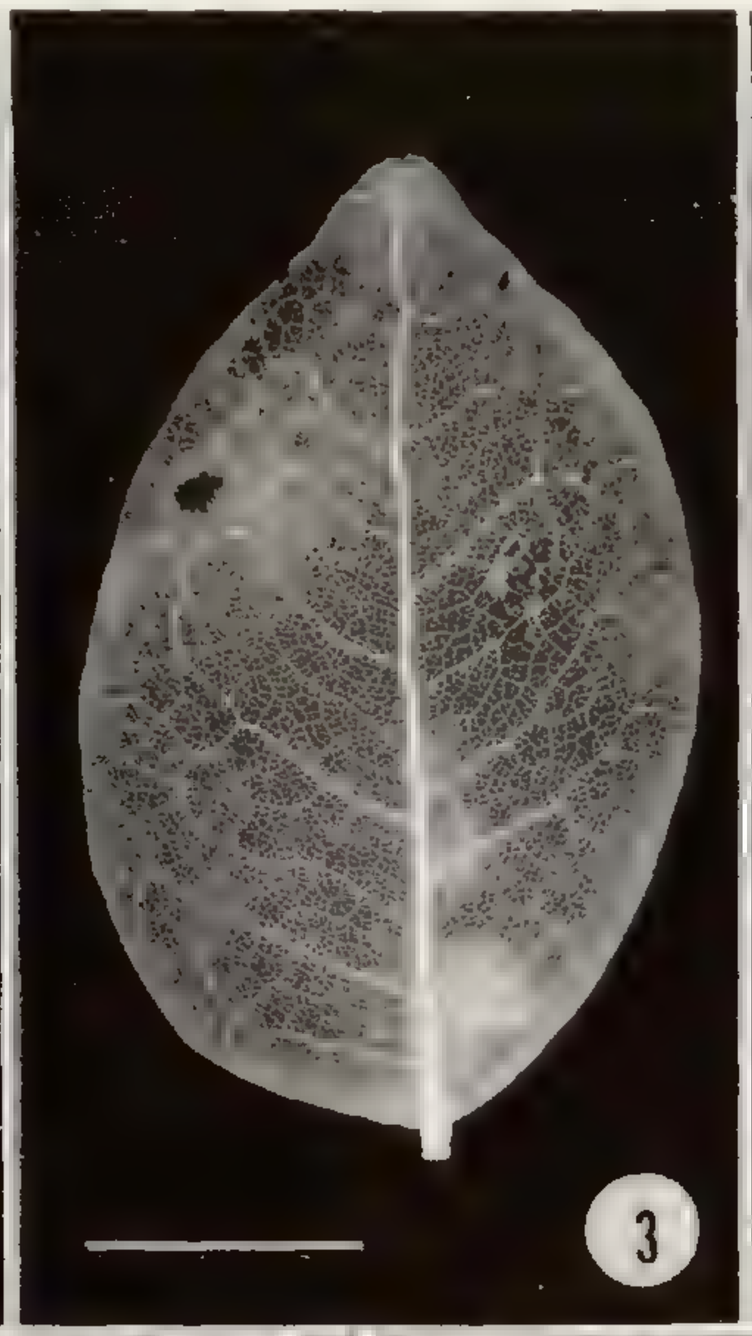
This report is based on first-hand examination of 97 leaf and 87 wood specimens of 61 species of Oldfieldioideae. Specimens examined are listed in Appendix 1. The specimens available represent to some degree all genera of the subfamily except *Croizatia* and *Paradrypetes*; it should be noted that leaves of *Voatamalo* and wood of *Kairothamnus*, *Scagea*, and *Stachystemon* are lacking in this study. Previous anatomical literature concerning genera of Oldfieldioideae provided by the publications listed in Appendix 2 has been incorporated into the following account as appropriate.

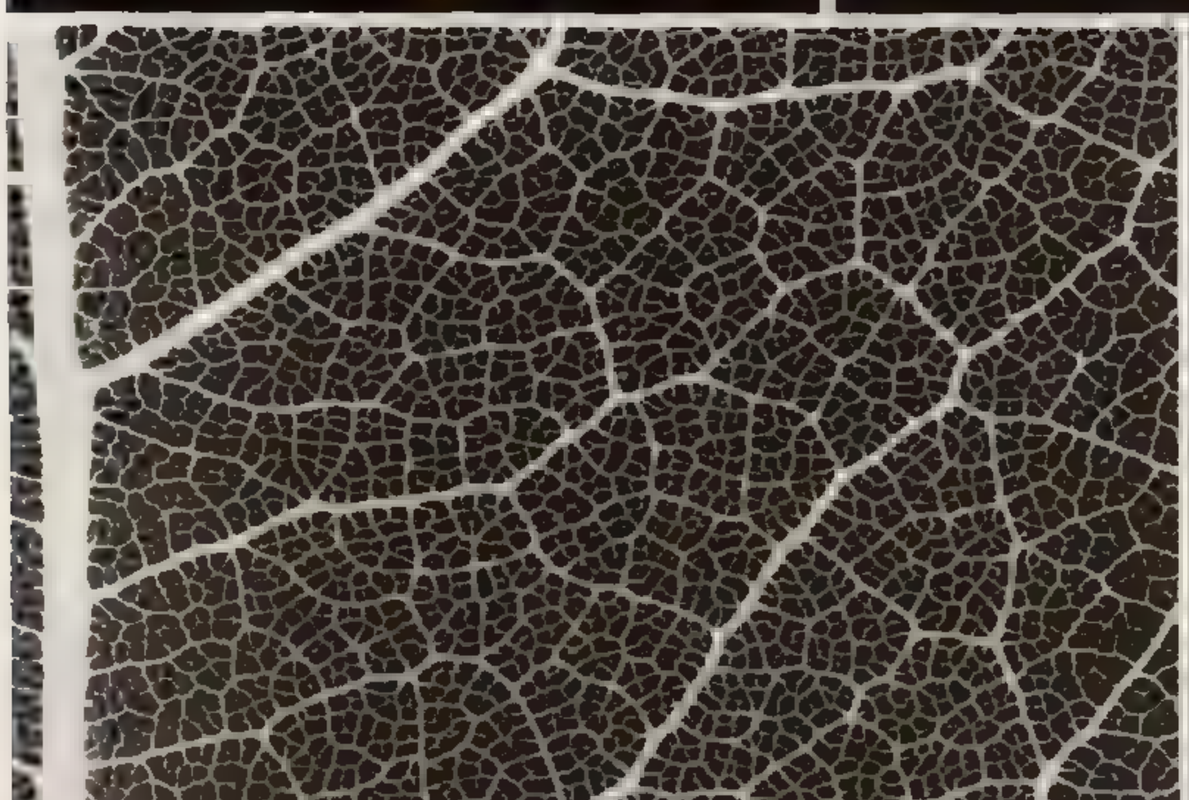
Leaf Architecture

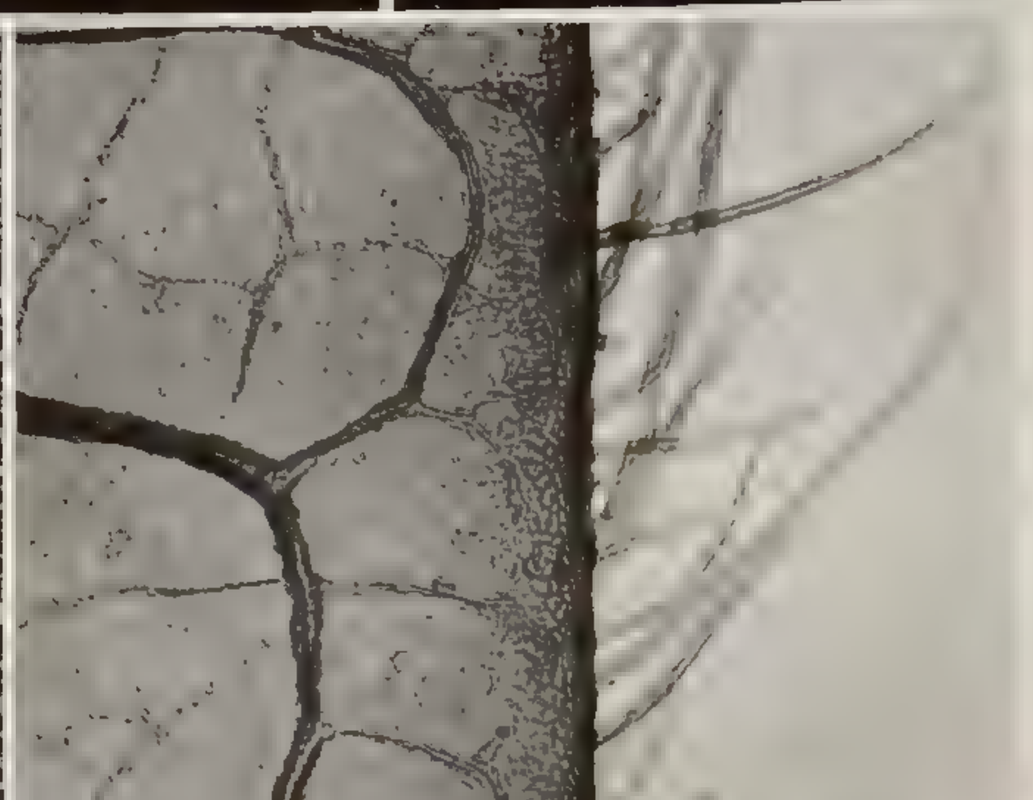
For the most part, leaves are either simple or palmately compound; however, interesting transitional morphologies do exist. Leaves of *Oldfieldia* are palmately compound, with 3–8 leaflets; those of *Celaenodendron*, *Picrodendron*, and *Piranhea* are trifoliolate; both palmately compound and simple leaves occur in *Aristogeitonia*; and leaves of *Parodiodendron* Hunz. are unifolioate, as evidenced by the minute stipels at the apex of the petiole (Hunziker, 1969) and by the frequent disarticulation of the lamina at the same point (Fig. 4). Finally, leaves of *Micrantheum*, which occur in alternate groups of three (to five), have been interpreted as the leaflets of a palmately compound leaf which, by loss of their common petiole, are sessile on the stem (Baillon, 1858); alternatively, this unique phyllotaxy has been attributed to foliate stipules (Grüning, 1913; Webster & Miller, 1963). For the most part, leaf margins are entire, the few exceptional species being *Austrobuxus cuneatus* (Airy Shaw) Airy Shaw, *A. swainii* (de Beuzev. & C. T. White) Airy Shaw, *Choriceras tricorne* (Benth.) Airy Shaw (Figs. 7, 8), *Dissiliaria muelleri* (Baill.) ex Benth., *Paradrypetes ilicifolia* Kuhlm. (Levin, 1986), *P. subintegrifolia* G. Levin (Levin, 1992), *Tetracoccus dioicus* Parry (only some leaves), and *T. ilicifolius* Coville & Gilman. *Paradrypetes* possesses irregularly spaced spinose teeth (Levin, 1986, 1992). Teeth of *Tetracoccus ilicifolius* are the largest in the subfamily: median veins of these teeth are derived from the looped secondary veins; there are prominent brochidodromouslike loops within the tooth itself; and median veins extend nearly to the apices, which in the specimens examined appear to possess apical caps, at least in young leaves. Teeth of the remaining species are much smaller, consisting of a vein ending in a small protrusion of leaf tissue. Significantly, however, deciduous apical caps are also visible in *Austrobuxus swainii* and *Choriceras tricorne* (Figs. 7, 8). Tooth morphology in Oldfieldioideae thus conforms with the theoid type (Hickey & Wolfe, 1975). Excluding noninformative spinose teeth, theoid teeth are the only type found in Phyllanthoideae, specifically in the genera *Drypetes* Vahl, *Putranjiva* Wall., and *Bischofia*; reduced theoid teeth are also present in Aporuseae (Levin, 1986).

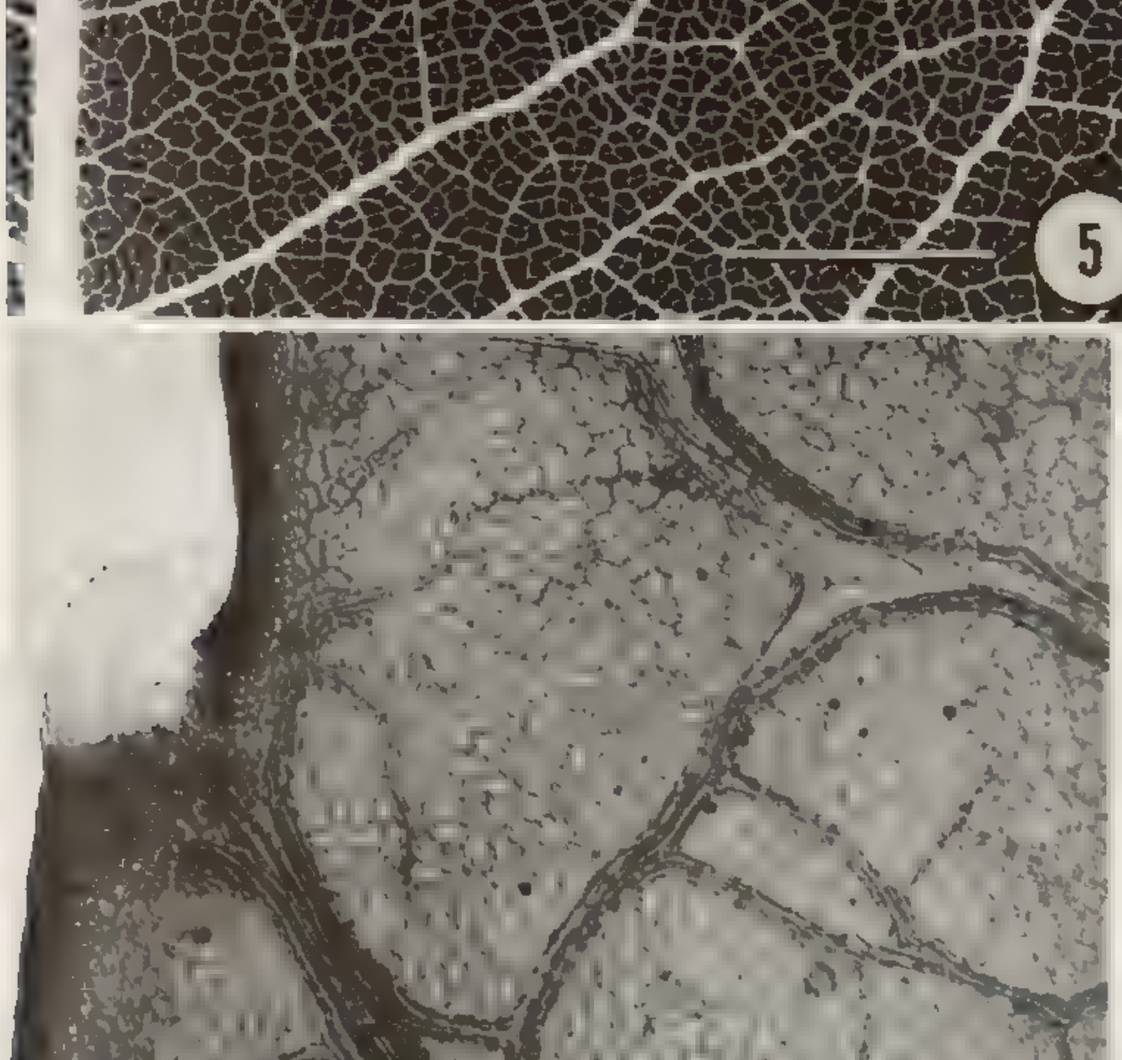
Venation is always pinnate, most frequently festooned brochidodromous (Figs. 2, 3). In addition to brochidodromy, however, leaves of *Longetia*

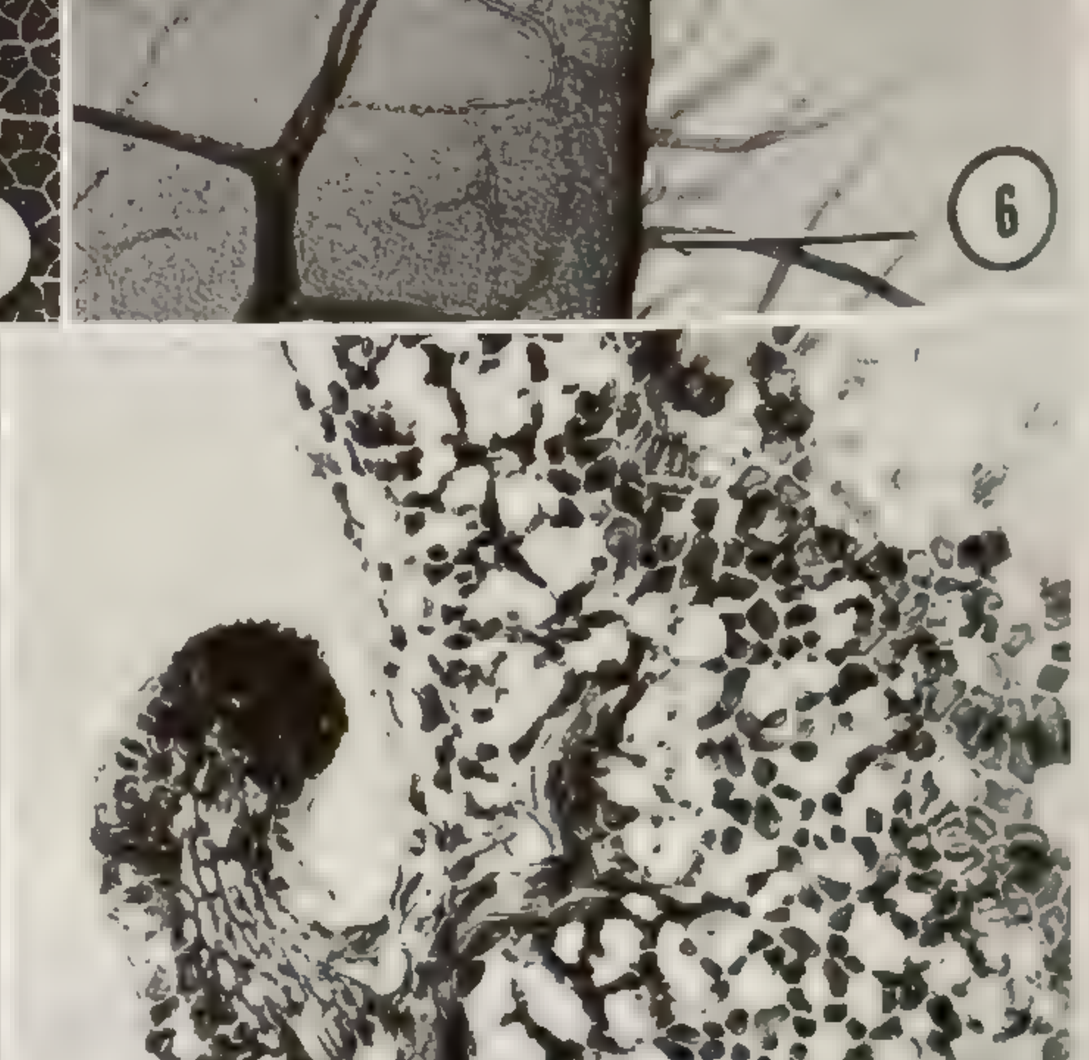












FIGURES 2–8. Leaf architectural features of Oldfieldioideae. —2. *Austrobuxus rubiginosus* (*Baumann-Bodenheim 15010*), cleared leaf, bar = 1 cm.—3. *Celaenodendron mexicanum* (*Ortega 6367*), cleared leaf, bar = 1 cm.—4. *Parodiodendron marginivillosum* (*Hueck 469*), cleared leaf, note disarticulation of petiole from base of lamina, bar = 5 mm.—5. *Picrodendron baccatum* (*Gillis 6963*), note lack of vein orders beyond tertiaries, bar = 2.5

exhibit a tendency toward eucamptodromy whereas those of *Dissiliaria*, *Petalostigma*, *Picrodendron*, and *Tetracoccus* tend toward reticulodromy. Leaves of the Australian genera of Pseudanthinae (Caletieae sensu stricto) exhibit a continuum of increasing disorganization, presumably a consequence of xeromorphy: in *Neoreopera* leaves are weakly festooned brochidrodromous; in *Micrantheum* one can find vestiges of brochidodromous venation as well as secondary veins that recurve and ramify or form a weak reticulum; in *Stachystemon* the range is from reticulodromous to kladodromous; and in *Pseudanthus* leaves are all kladodromous (Fig. 9). Primary veins are mostly of moderate size, but, especially in xeromorphic leaves, they may range to stout and massive, e.g., those of *Hyaenanche*, *Tetracoccus*, and the Australian Pseudanthinae (Fig. 9). Intersecondary veins are usually absent, although one or two simple intersecondaries per intercostal area occur occasionally in *Austrobuxus* and *Mischodon*, and routinely in *Croizatia* (Levin, 1986), *Oldfieldia*, *Paradrypetes* (Levin, 1986), *Piranhea*, and *Podocalyx*. Intersecondary veins are frequent in several primitive Phyllanthoideae, namely, *Amanoa* Aubl., *Blotia* Leandri, *Heywoodia* Sim, *Petalodiscus* Baill., *Savia* Willd., and *Wielandia* Baill. (Levin, 1986); their presence is thus postulated to be primitive for Oldfieldioideae. Tertiary vein patterns are usually random reticulate; ramified patterns occur in *Hyaenanche*, species of *Austrobuxus*, and those species of Australian Pseudanthinae that possess distinguishable tertiaries; there is a slight tendency toward transverse tertiaries in *Parodiodendron*, *Paradrypetes* (Levin, 1986), *Petalostigma*, and *Podocalyx*; and the tertiary veins of *Piranhea* have a slight tendency to form orthogonal patterns. Marginal venation is incomplete (Fig. 11) or looped (Fig. 6) in many genera, "hemmed" with a fimbrial vein in the genera with compound leaves (Figs. 10, 12) plus *Dissiliaria* and *Mischodon*, or dominated by a massive intramarginal vein in most Australian Pseudanthinae (Fig. 9). A distinctive furcate-flabellate form of marginal venation occurs in *Hyaenanche*.

High-order venation varies considerably within Oldfieldioideae. Perhaps most notable is the occurrence of ultimate reticula in which vein order is not distinguishable, a feature of *Celaenodendron*, *Picrodendron* (Fig. 5), and *Piranhea* (all New World genera with trifoliolate leaves) plus *Androstachys*; this character state is extremely rare in the dicots as a whole (L. J. Hickey, pers. comm.) and is thus a potentially robust synapomorphy linking these genera. Areoles are well developed in the genera with compound leaves (Figs. 5, 12) plus *Dissiliaria*, *Mischodon*, *Parodiodendron* (Fig. 6), and *Podocalyx*; otherwise, areoles are imperfectly developed. Areoles are usually arranged randomly, but are oriented in *Celaenodendron* and somewhat oriented in *Picrodendron*, *Piranhea*, and *Dissiliaria*. Veinlets are usually present and mostly simple or branched; the degree of branching varies widely, tending to be most highly branched in leaves with low regularity of tertiary and higher order veins. Veinlets are absent in *Androstachys* (Fig. 12), but they may appear to be present upon superficial examination because of the columnar sclereids located in each areole (see below).

Leaf Anatomy

Trichomes have been observed in about two-thirds of the genera of Oldfieldioideae. Many species are glabrescent with age, although mature leaves of *Androstachys*, *Parodiodendron*, and species of *Petalostigma*, for example, are clearly pubescent. Trichomes are either simple unicellular or uniseriate, generally consisting of less than six cells. Within Pseudanthinae, epidermal emergences range from small papillae to four-celled uniseriate trichomes. The densely packed trichomes of *Androstachys johnsonii* Prain, which consist of a short basal cell and long curly terminal cell, have been suggested by Alvin (1987) to function in absorption of atmospheric moisture (mists and drizzles) in the otherwise extremely arid environment of southern Africa. *Oldfieldia* possesses trichomes similar to those of *Androstachys*, arguing for some degree of relationship between these two genera despite their manifest differences in reproductive morphology. Depending on the species, trichomes of *Austrobuxus* are either simple or bifurcate (malpighiaceous). *Parodiodendron* is unique within the subfamily in possessing strongly ciliate leaf margins (Fig. 6). Rao & Raju (1985) reported uniseriate, stellate, and glandular hairs in *Dissiliaria*, characteristics reminiscent of uniovu-

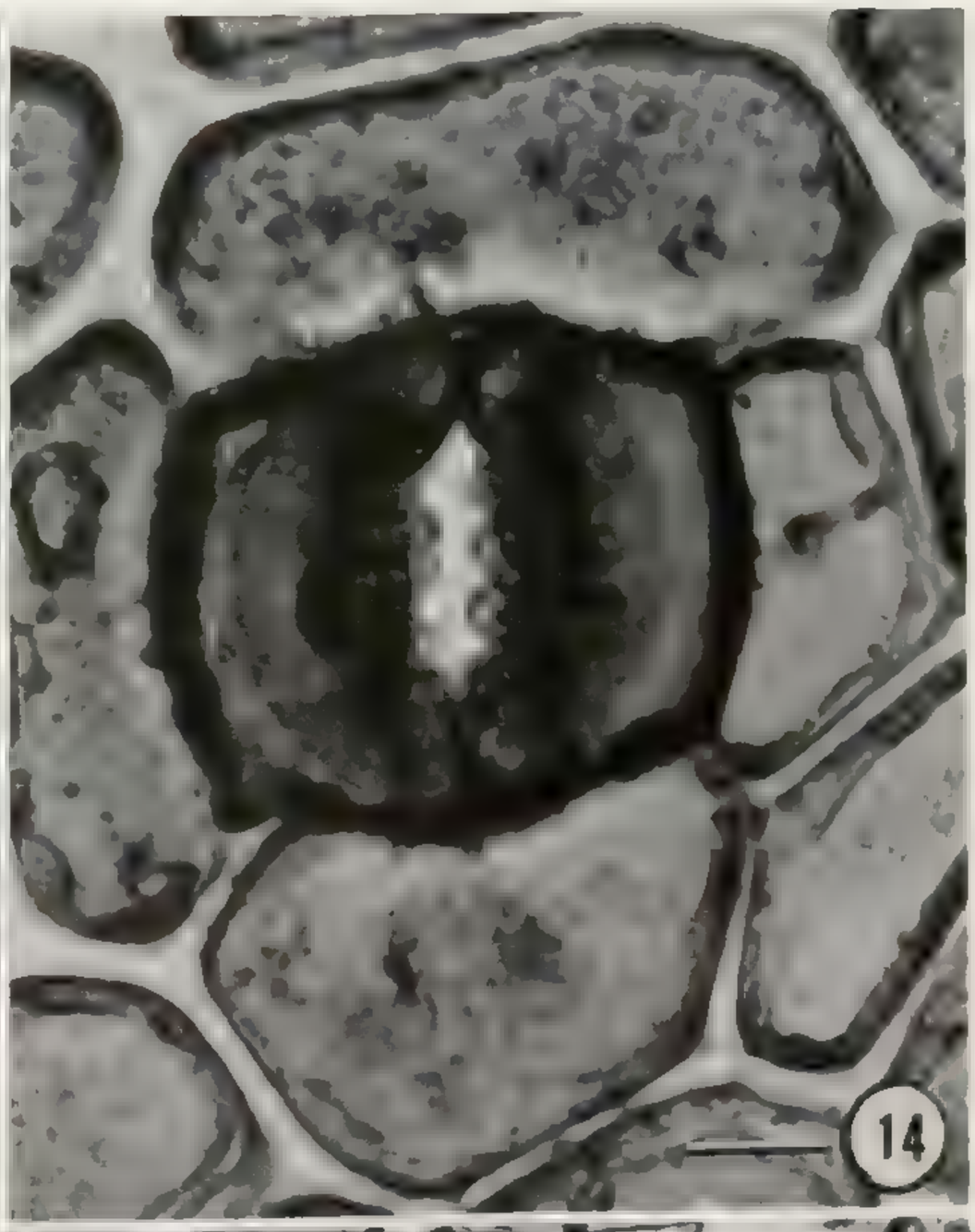
←

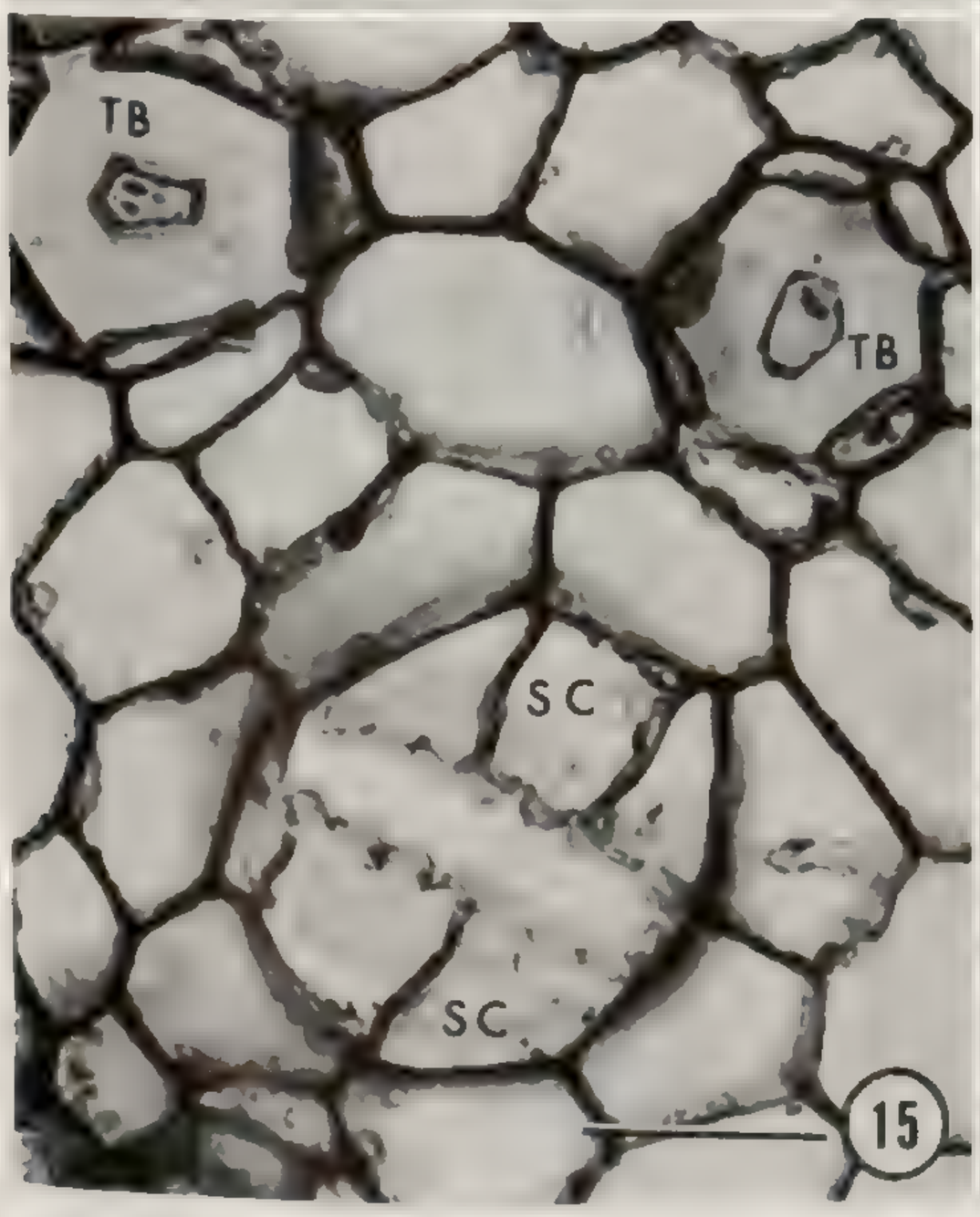
mm.—6. *Parodiodendron marginivillosum* (*Hueck 469*), margin of cleared leaf, bar = 250 μm.—7. *Choriceras tricorne* (*Forman s.n.*), tooth at margin of cleared leaf, bar = 250 μm.—8. *Choriceras tricorne* (*Forman s.n.*), paradermal section through tooth at leaf margin, note glandular apex, bar = 100 μm.

FIGURES 9–12. Leaf architecture of Oldfieldioideae.—9. *Pseudanthus orientalis* (*Clemens 44092*), kladodromous venation, massive primary and intramarginal veins, bar = 250 μm.—10. *Celaenodendron mexicanum* (*Ortega 6367*), fimbrial vein (far right), bar = 250 μm.—11. *Petalostigma banksii* (*Perry 1981*), branched veinlets with swollen ultimate tracheids, bar = 100 μm.—12. *Androstachys johnsonii* (*Wellcome Chemical Research Laboratory s.n.*), well-developed areoles with columnar sclereids, veinlets absent, bar = 1 mm.

late euphorbs that would be unique to Oldfieldioideae; however, neither trichomes nor their bases were detected in the leaves available to me.

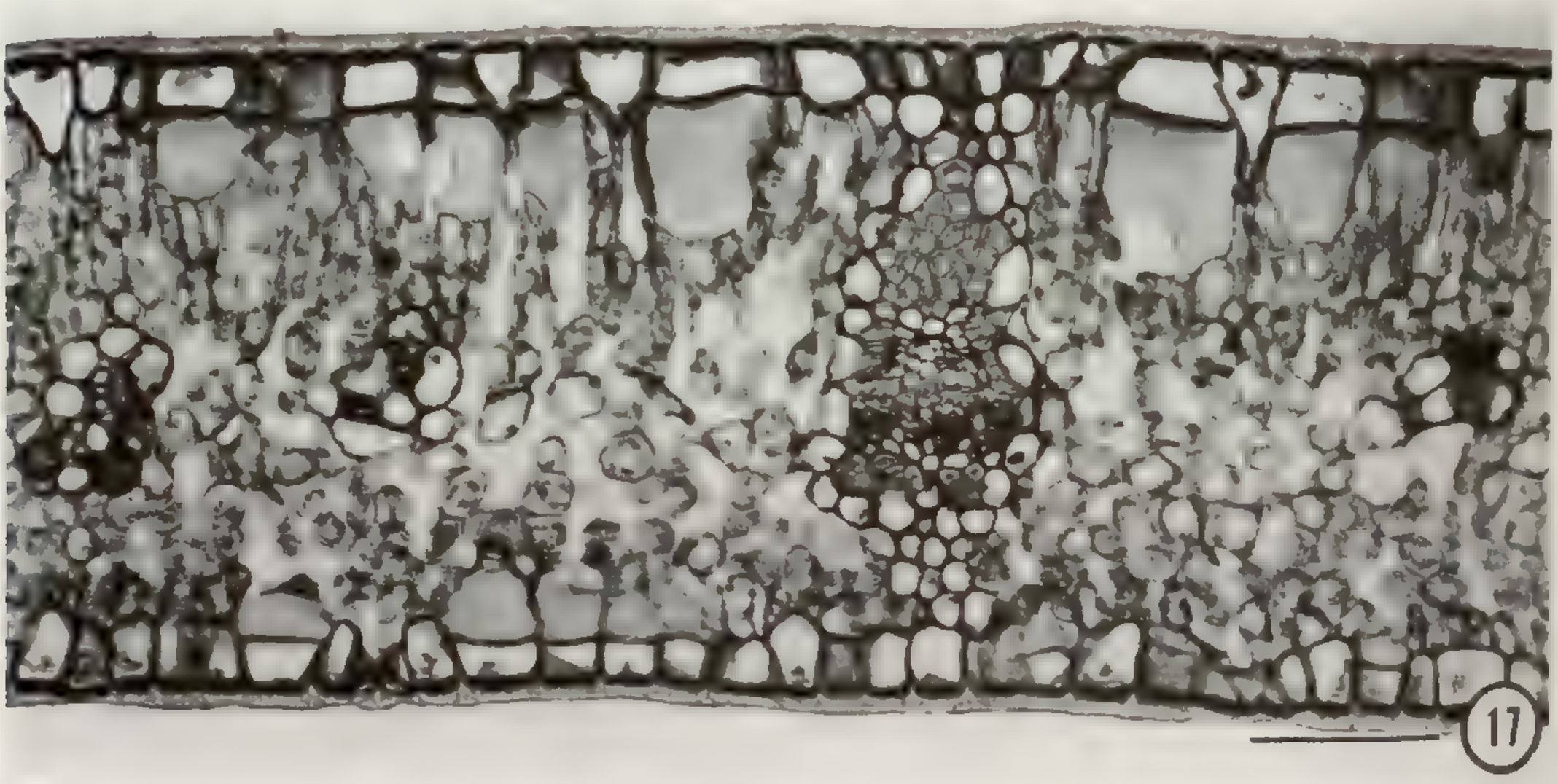
The epidermis is fundamentally uniseriate. However, a single layer of hypodermis has been reported for *Paradrypetes* (Milanez, 1935) and some or all epidermal cells of the Australasian genera have a horizontal partition resulting in a poorly to well-defined hypodermis (Figs. 17–19). The inner cell or chamber thus formed contains mucilage, which is common in other genera as well. Expansion of the mucilaginous layer in Australian Pseudanthinae greatly distends the adaxial epidermis (Figs. 18, 19); while the grossly expanded mucilaginous layer may well be an artifact of preparation, it is derived solely from the lower portions of subdivided epidermal cells and is not thickly multicellular as depicted by Gaucher (1902), whose erroneous in-

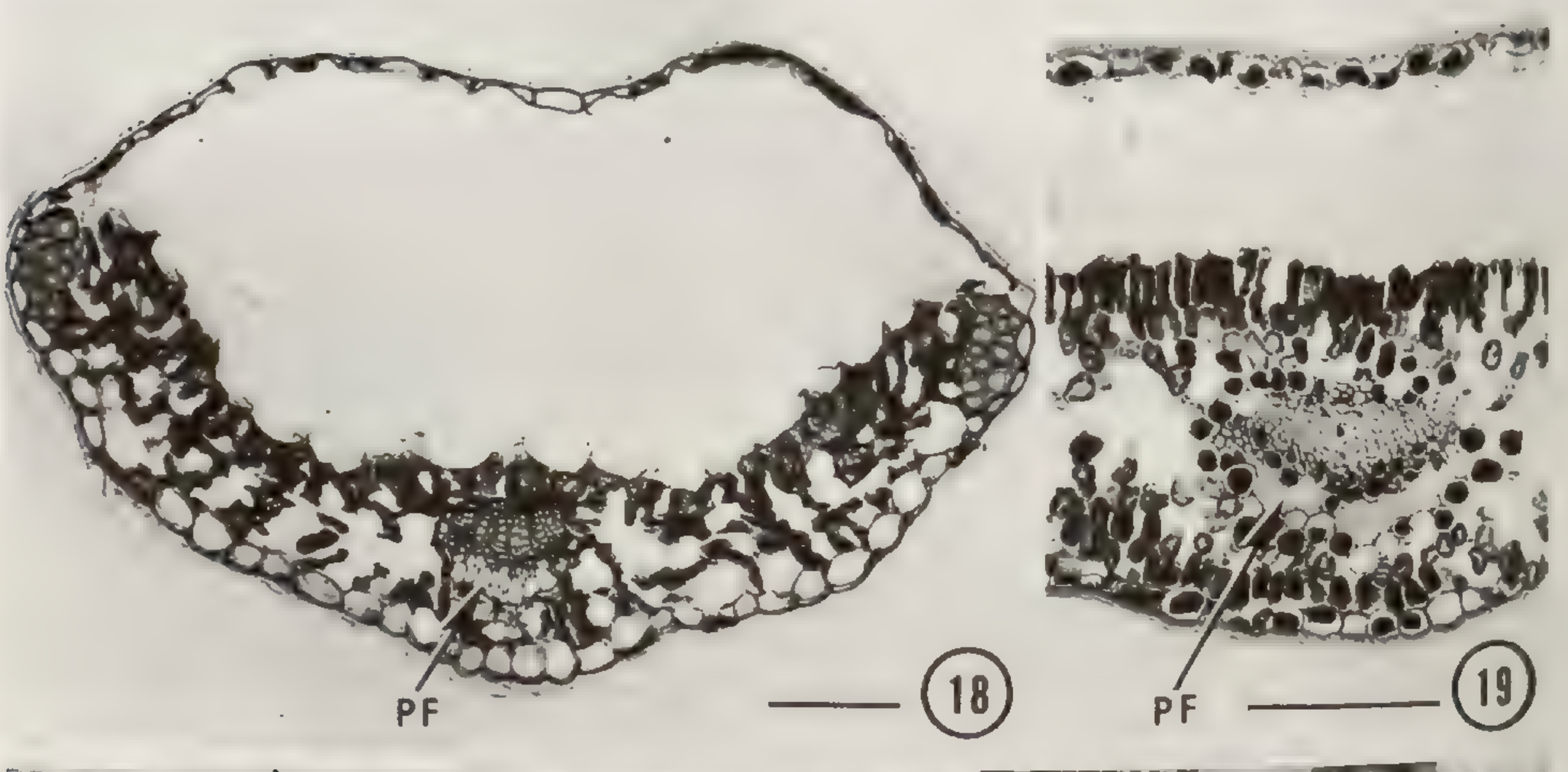


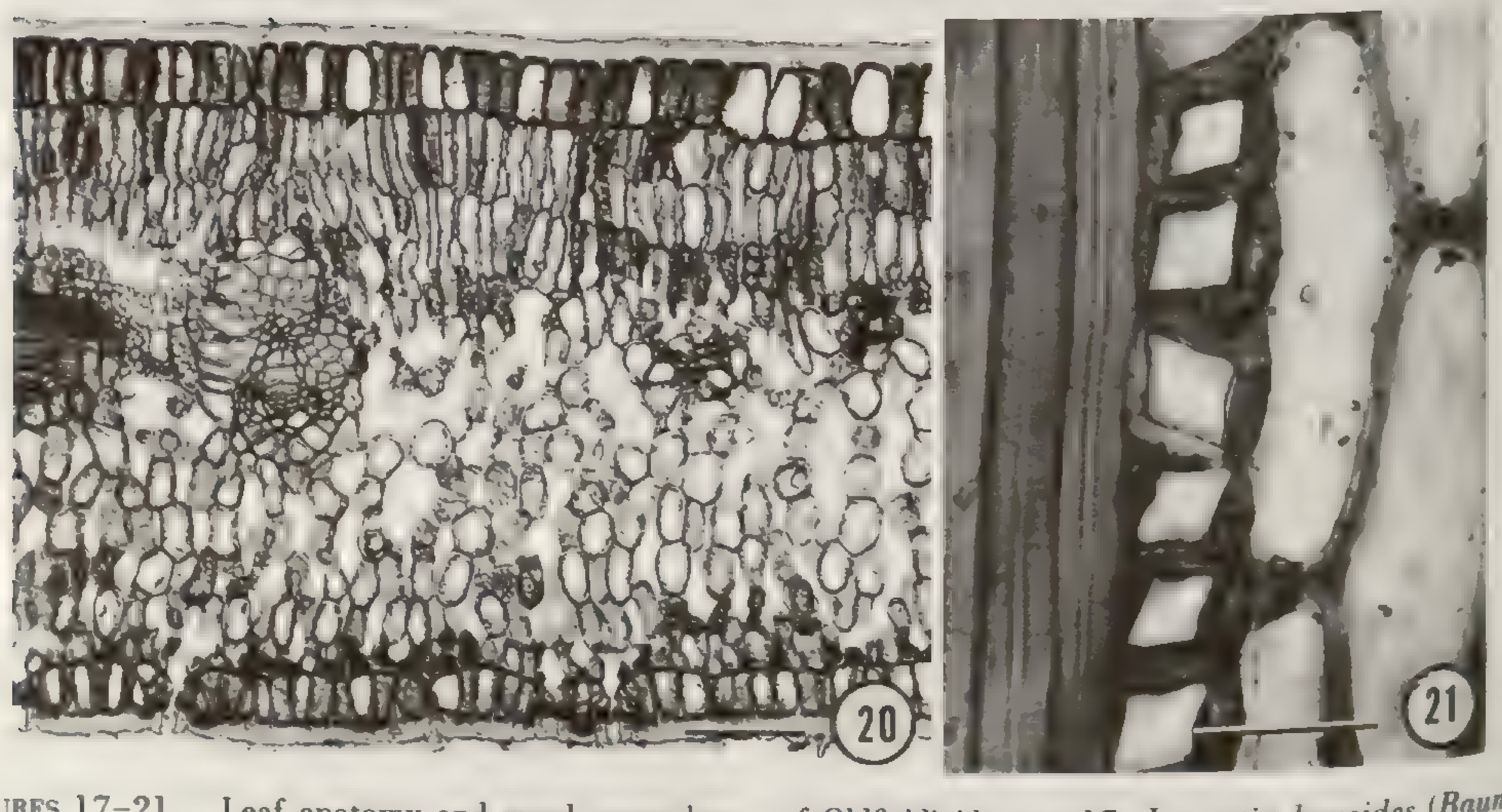


FIGURES 13-16. Leaf anatomy of Oldfieldioideae.—13. *Longetia buxoides* (*Baumann-Bodenheim 5605*), stomate from cross section, bar = 20 μm.—14. *Scagea oligostemon* (*McKee 2352*), surface view of stomate from paradermal section, note crenulate inner anticlinal walls of subsidiary cells visible through stomatal aperture, bar = 10 μm.—15. *Austrobuxus huerlimannii* (*McKee 4850*), subdivided crenulate subsidiary cells and trichome bases from paradermal section, bar = 20 μm.—16. *Podocalyx loranthoides* (*Krukoff 811*), tracheoid idioblasts from macerated mesophyll, bar = 20 μm. GC = guard cell, SC = subsidiary cell, TB = trichome base.

terpretation has been reiterated by others (e.g., Metcalfe & Chalk, 1950; Raju & Rao, 1977). So far, no mucilage has been detected in *Aristogeitonia*, *Celaenodendron*, *Mischodon*, *Piranhea*, and *Podocalyx*. Mucilaginous epidermis is known in several Phyllanthoideae, for example, *Actephila* Bl., *Antidesma* L., *Aporusa* Bl., *Amanoa*, *Baccaurea* Lour., *Bridelia* Willd., *Hyeronima* Fr. Allem, *Phyllanthus* L., *Richeria*, and *Savia* (Metcalfe & Chalk, 1950). In surface view, anticlinal walls of epidermal cells are generally straight (Figs. 14, 15), the only exceptions being *Aristogeitonia*, *Celaenodendron*, *Piranhea*, (all members of Picrodendreae), and *Dissiliaria*, in which these walls have a wavy outline; intriguingly, paradermal sections of *Aristogeitonia* and *Celaenodendron* reveal







FIGURES 17–21. Leaf anatomy and wood parenchyma of Oldfieldioideae.—17. *Longetia buxoides* (*Baumann-Bodenheim 5605*), leaf cross section, note chambered mucilaginous epidermal cells, bar = 100 μm.—18. *Pseudanthus orientalis* (*Wilson 679*), leaf cross section, note grossly expanded mucilaginous hypodermis and prominent intramarginal veins, bar = 100 μm.—19. *Micrantheum hexandrum* (*McGillivray 3196*), cross section of primary vein, note grossly expanded mucilaginous hypodermis, bar = 100 μm.—20. *Hyaenanche globosa* (*Godfrey SH 12571*), cross section of leaf, bar = 100 μm.—21. *Piranhea trifoliata* (*Ducke s.n., USw 31485*), normal and chambered crystalliferous axial xylem parenchyma cells, bar = 15 μm. PF = phloem fibers.

the inner portions of epidermal cells to possess straight anticlinal walls.

Leaves are overwhelmingly hypostomatic, although both hypo- and amphistomatic conditions occur in species of *Petalostigma* and *Tetracoccus*. Stomatal type is anomocytic in *Podocalyx*, paracytic in *Paradrypetes* (Levin, 1986), but otherwise brachyparacytic (Fig. 14) or derived from a brachyparacytic pattern. For example, intruding lobes of adjacent cells tend to form an anomocytic pattern in *Tetracoccus* as viewed from the surface; paradermal sections, however, reveal typical brachyparacytic configurations. The most frequent modification of stomatal type is the tendency for one or both of the subsidiary cells to become subdivided into two or three smaller cells; subdivision of subsidiary cells may be a consistent feature in a given taxon, or it may be sporadic, affecting only some stomata or only one subsidiary cell of a given pair. Subdivided brachyparacytic stomata occur in *Androstachys*, where the pattern has been described as incompletely cyclocytic (Alvin, 1987), *Aristogeitonia*, some species of *Austrobuxus* (Fig. 15), *Hyaenanche*, *Mischodon*, *Picrodendron*, and *Pseudanthus*. The paracytic stomata of *Paradrypetes* are also subdivided in a similar fashion (Levin, 1986). The distribution of subdivided subsidiary cells does not follow any obvious taxonomic grouping within the subfamily. Within Phyllanthoideae, brachyparacytic stomata are characteristic of Bridelieae, Drypeteae, Phyllantheae–Fleuggeinae, and certain genera of Wielandieae; moreover, subdivided brachyparacytic stomata occur in *Lachnostylis* Turcz. and *Bridelia* (Levin, 1986). Raju & Rao (1977) reported brachyparacytic stomata to be the most common type among woody genera throughout Euphorbiaceae.

In most genera subsidiary cells extend partially over the inner periclinal walls of adjacent guard cells in a "semi-piggyback" fashion (Fig. 13); the inner anticlinal walls of subsidiary cells thus delimit an inward extension of the stomatal pore. Within Phyllanthoideae, Levin (1986) noted a similar spatial relationship of guard and subsidiary cells only in *Drypetes*. The inner anticlinal walls of "piggyback" subsidiary cells may have crenulate outlines (Figs. 14, 15), a feature first observed by Solereder (1908) in *Micrantheum* and *Pseudanthus* that now proves characteristic of the Australasian genera (*Mischodon* and certain species of *Austrobuxus* excluded) plus the South African genus *Hyaenanche*; this feature defines a distinct clade within the subfamily. Crenulate subsidiary cells are only weakly developed in the single specimen of *Whyanbeelia* available for study. In contrast to most genera, subsidiary and guard cells are coplanar in *Oldfieldia* and *Parodiodendron*.

Mesophyll is bilateral except in some species of *Petalostigma* with isobilateral leaves; leaves of *Hyaenanche* approach an isobilateral condition (Fig. 20). Spongy mesophyll with well-developed intercellular spaces but a tendency toward vertical alignment of cells occurs in *Androstachys*, *Oldfieldia*, *Picrodendron*, and *Piranhea*, all members of Picrodendreae. Mesophyll usually contains scattered druses; prismatic crystals are also present in *Aristogeitonia*, *Austrobuxus*, *Dissiliaria*, *Hyaenanche*, *Longetia*, and *Micrantheum*. Mesophyll of *Paradrypetes* contains raphide bundles (Milanez, 1935; Levin, 1986), a structure otherwise unknown in Euphorbiaceae (Gaucher, 1902; Metcalfe & Chalk, 1950). No crystals were observed in the mesophyll of *Celaenodendron*, *Parodiodendron*, and *Piranhea*. Except for *Androstachys* and *Stachyandra*, foliar sclereids are absent; areoles of these genera usually contain a single columnar sclereid with ramified tips that run parallel with the bases of epidermal cells and eventually intermingle with trichome bases and the bundle sheath extensions of the veins. Alvin (1987) has interpreted the sclereids of *Androstachys* to function in apoplastic transport from its water-absorbant trichomes. It is intriguing to speculate that the vertically oriented spongy mesophyll cells of *Androstachys* may have served as a preadaptation for the evolution of its columnar sclereids. Another unique mesophyll feature is found in *Podocalyx*, which bears unbranched, sinuous tracheoid idioblasts with spirally thickened, nonlignified walls (Fig. 16). These elements, occurring most frequently between the junction of palisade and spongy layers, are sufficiently abundant to obscure the presence of veinlets in clearings; they are not, however, directly connected to any vasculature.

Vasculature of the primary vein consists of adjacent (colateral) regions of xylem, phloem, and phloem fibers. Little taxonomic significance can be read into the overall configuration of primary vein vasculature, which ranges from broad shallow arcs to more tightly curved u-shaped arcs to closed loops; reduced leaves of desert xerophytes, however, tend to have patterns with minimal curvature (Figs. 18, 19). Phloem fibers of the primary vein in *Petalostigma* and the Australian Pseudanthinae are unlignified (Figs. 18, 19), in sharp contrast to the usual lignified condition of these cells in the rest of the subfamily. Smaller veins are frequently associated with a parenchymatous bundle sheath (Fig. 17). Bundle sheath extensions that are merely parenchymatous occur in *Longetia* (Fig. 17); crys-

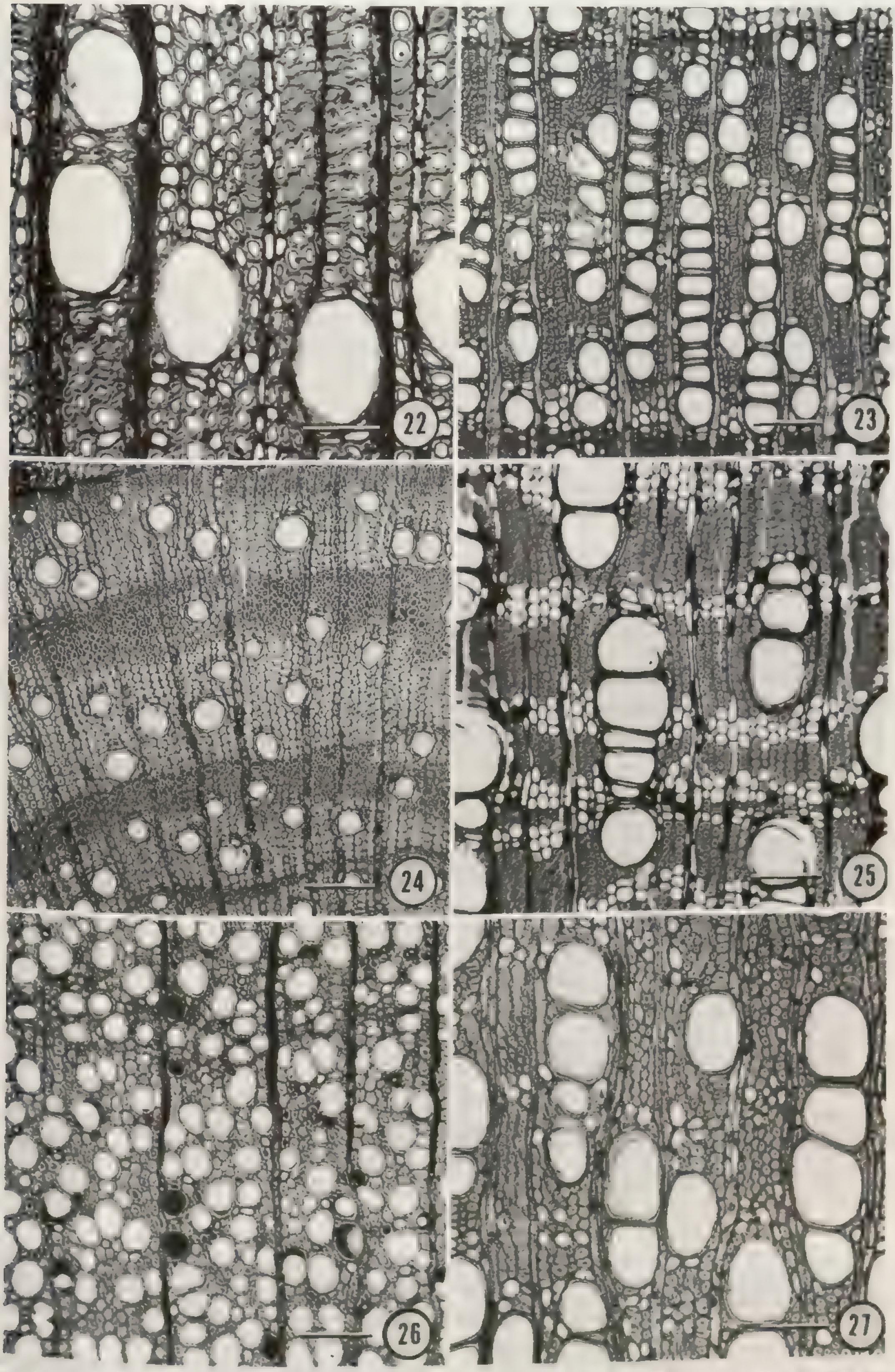
tals are present in bundle sheath extensions of *Aristogeitonia*, *Celaenodendron*, *Hyaenanche*, *Mischodon*, *Oldfieldia*, *Parodiodendron*, *Petalostigma*, *Picrodendron*, and *Piranhea*; and at least some fibrous elements are also present in those of *Androstachys*, *Mischodon*, and *Piranhea*. Overall, bundle sheath extensions seem best developed in the genera bearing compound leaves, but also occur sporadically elsewhere in the subfamily. Swollen terminal tracheids of veinlets occur in some *Austrobuxus*, *Choriceras*, *Hyaenanche*, *Longetia*, *Petalostigma* (Fig. 11), and *Tetracoccus*.

Wood Anatomy

Growth rings are often absent or only faintly visible. Growth rings are present, however, in *Androstachys*, *Celaenodendron* (Fig. 23), *Parodiodendron*, *Petalostigma*, *Podocalyx*, *Tetracoccus*, and Australian Pseudanthinae (Fig. 24); except for *Podocalyx*, from the upper Amazon and Orinoco drainage basins, these are plants of dry habitats with strongly seasonal availability of moisture. Pores are evenly distributed (i.e., diffuse porous in species with growth rings), except in the ring porous wood of *Tetracoccus*, which extends into desert regions of western North America. Pore outlines are mostly circular, generally small, and usually less than 100 μm diam.; pore diameters are often less than 50 μm in the genera mentioned above from dry habitats. Perforation plates are overwhelmingly simple, but scalariform plates are found in *Paradrypetes* (exclusively so according to Mennega (1987), mixed with simple perforations according to Araujo & Mattos Filho (1984)) and mixed simple, scalariform (Fig. 30), and reticulate plates characterize *Podocalyx*. Intervascular pits are transitional in *Paradrypetes* and *Podocalyx*; otherwise they are alternate and mostly small, ca. 5 μm or less. Very small intervascular pits (2–3 μm) are found in *Aristogeitonia*, *Neoroepera*, and *Pseudanthus*; somewhat larger than usual pits (6–8 μm) occur in *Austrobuxus*, *Celaenodendron*, *Parodiodendron*, *Picrodendron*, *Piranhea*, and *Podocalyx*. Vessel element lengths for most genera fall within the range of 400–700 μm; vessel elements are somewhat shorter in *Picrodendron* (ca. 300 μm), somewhat longer in *Dissiliaria* (ca. 800 μm), *Austrobuxus* (ca. 950 μm), and *Paradrypetes* (ca. 1200 μm), and longest in *Podocalyx* (ca. 1250 μm). Sculpture on the inner surface of vessels is rare; some vessels of *Choriceras* possess spiral thickenings; thickenings are characteristic of *Whyanbeelia* (spiral only) and *Tetracoccus* (spiral to reticulate). Tyloses and/or tannins are common in lumina of heartwood vessels; silica deposits occur in lumina of *Whyanbeelia*.

Imperforate tracheary elements bear either simple or bordered pits. Elements with simple pits, i.e., libriform wood fibers, characterize the genera with compound leaves (*Aristogeitonia*, *Celaenodendron*, *Oldfieldia*, *Piranhea*, and *Picrodendron*) plus *Dissiliaria*, *Hyaenanche*, and *Petalostigma*; some of these may also possess elements with bordered pits. The remaining genera possess only elements with bordered pits; these cells are probably best characterized as fiber-tracheids by virtue of their relatively small pit borders and thick walls. However, because intervascular pits in some oldfieldioids are remarkably small, *Androstachys*, *Aristogeitonia*, and the Australian genera of Pseudanthinae, for example, pits of imperforate elements may be approximately equal to or slightly larger than intervascular pits in the same wood; by the criteria of Bailey (1936) such elements would be tracheids, by definition, despite their thick walls and pit diameters of 5 μm or less. "Tracheid," with its connotation of primitive conducting element, hardly seems appropriate for such cells. On the other hand, the tracheids of *Podocalyx*, with pit diameters up to 13 μm, attest more convincingly to primitive structure, and both fiber-tracheids and tracheids are present in *Austrobuxus*, distinguishable by both wall thickness (Fig. 22) and pit size. Bands of gelatinous fibers occur in woods of Australian Pseudanthinae (Fig. 24), *Hyaenanche*, and *Tetracoccus*. Imperforate elements often possess such thick cell walls that lumina appear completely closed; Bamber (1974) noted that these thick-walled fibers lack an easily detectable S3 layer in *Austrobuxus*, *Dissiliaria*, and *Petalostigma*. Fibers are septate only in *Parodiodendron*.

Rays are numerous, generally more than 15 per mm; however, there are more than 20 per mm in Australian Pseudanthinae, and only 12 per mm in *Androstachys* and *Oldfieldia*. High ray frequencies are probably related to the general narrowness of individual rays. Rays are mostly 1-, 2-, or 3-seriate, but up to 4- or 5-seriate rays occur in *Choriceras*, *Dissiliaria*, *Aristogeitonia*, and *Tetracoccus* (Fig. 33). Polymerous (vertically fused) rays are usually common (Fig. 32); however, they are infrequent or absent in *Androstachys* (Fig. 31), *Choriceras*, *Parodiodendron*, *Tetracoccus*, and the Australian Pseudanthinae. Aggregate rays were observed in *Choriceras* only. Rays are usually heterocellular (Figs. 28, 29), which is generally considered the primitive condition. Homocellular procumbent rays are shared by *Androstachys* and



FIGURES 22–27. Wood anatomy of Oldfieldioideae. —22. *Austrobuxus swainii* (*deBeuzeville s.n., MADw 10449*), note thin- and thick-walled fibers. —23. *Celaenodendron mexicanum* (*Ortega 35, USw 3886*), note long radial multiples of pores and boundaries of growth ring (top and bottom). —24. *Micrantheum hexandrum* (*Whaite & Whaite 3536*), note bands of gelatinous fibers. —25. *Piranhea trifoliata* (*Ducke s.n., USw 31485*), note banded distribution of axial xylem parenchyma. —26. *Androstachys johnsonii* (*Pretoria UND 2127, Uw 21991*). —27. *Oldfieldia africana* (*Cooper 88, USw 4517*). All bars = 100 μm.

TABLE 1. Wood structure of biovulate euphorbs, after Metcalfe & Chalk (1950).

Feature	*Aporusa*-type	"Other genera"	*Glochidion*-type
Perforations	scalariform, simple, or both	simple	simple
Fibers	nonseptate, thick-walled	nonseptate, thick-walled	septate, thin to moderately thick-walled
Parenchyma	abundant, diffuse or narrow bands	abundant, diffuse to wide bands	absent or scanty

some species of *Oldfieldia*, which serves to demonstrate that these woods are not as dramatically distinct as Metcalfe & Chalk (1950) suggested. Homocellular square to erect rays are one of several synapomorphies that mark the Australian genera of Pseudanthinae as a distinct monophyletic group. Vessel to ray pits are of two forms that appear to hold great systematic significance. The most distinctive pattern consists of highly irregular pits that range from circular to elongate with the elongate pits at various orientations: vertical, horizontal, or diagonal (Fig. 28). This irregular pattern is interpreted as primitive by virtue of its resemblance to primitive transitional intervascular pitting, and by its occurrence in *Paradrypetes* and *Podocalyx* (see below); irregular vessel-ray pits have been retained by all arborescent Australasian genera. All other genera possess uniform vessel-ray pits that are circular and alternate. If circular, alternate vessel-ray pits are indeed the derived character state, this feature evolved twice, since the Australian Pseudanthinae (i.e., Caletieae sensu stricto) are clearly derived from the lineage bearing the arborescent genera of Australasia (see below), rather than the lineage of African and American genera. Ray cells generally bear only tannins, but several exceptions occur: prismatic crystals are sporadic in *Podocalyx*, abundant in *Paradrypetes* (Araujo & Mattos Filho, 1984); silica deposits are common in *Petalostigma*; and sclerified cells bearing a prismatic crystal are abundant in *Aristogeitonia*, *Mischodon*, and *Tetracoccus fasciculatus*; these crystalliferous cells are only rarely present in *Voatamalo*. Perforated ray cells are sporadic in *Paradrypetes* (Milanez, 1935), *Podocalyx*, and *Hyaenanche*, but have not been observed in other Oldfieldioideae. Perforated ray cells are fairly widespread in Euphorbiaceae according to Giraud (1983), who recorded this feature in the following phyllanthoid genera: *Aporusa*, *Baccaurea*, *Bridelia*, *Cleistanthus* Hook. f. ex Planch., *Drypetes*, *Hyeronima*, and *Richeria*. Perforated ray cells are also present in *Putranjiva* (Nazma et al., 1981) and *Amanoa* (unpublished obs.).

Axial xylem parenchyma is mostly diffuse and diffuse-in-aggregates (Fig. 27), with bands also present in *Aristogeitonia*, *Dissiliaria*, *Parodiodendron* (strictly initial bands), *Picrodendron*, *Piranhea* (Fig. 25), and *Voatamalo*; on the other hand, parenchyma is infrequent and restricted to a few abaxial scanty paratracheal cells in *Androstachys*, *Stachyandra*, and the Australian genera of Pseudanthinae (Fig. 24). Parenchyma strands usually contain both ordinary cells and short sclerified cells bearing a single prismatic crystal (Fig. 21); crystalliferous parenchyma is absent, however, in *Paradrypetes*, *Podocalyx*, *Petalostigma*, *Whyanbeelia*, the Australian genera of Pseudanthinae, and most specimens of *Tetracoccus*. Since sclerified crystalliferous axial xylem parenchyma cells are common in several phyllanthoid woods (e.g., *Amanoa* and *Drypetes*), presence of such cells may be considered primitive for Oldfieldioideae; their loss may well be synapomorphous for *Petalostigma*, *Whyanbeelia*, and the Australian genera of Pseudanthinae; loss in others (e.g., *Paradrypetes*, *Podocalyx*, and most specimens of *Tetracoccus*) may represent convergent developments.

ORIGIN OF OLDFIELDIOIDEAE

EVIDENCE FROM WOOD ANATOMY

The analysis of wood structure of biovulate euphorbs contained in Metcalfe & Chalk (1950) provides a convenient starting point for discussion of relationships between Phyllanthoideae and Oldfieldioideae. In this work, three groups of genera were distinguished, as indicated in Table 1. At the most superficial of levels, woods of Oldfieldioideae, largely included in Metcalfe & Chalk's "other genera," may be characterized as a combination of the vessel features of *Glochidion*-type woods and the fiber and parenchyma features of *Aporusa*-type woods, the latter two categories consisting primarily of phyllanthoid genera. In some instances these three coarsely defined categories provide a useful perspective for placing genera; for example, the re-

moval of *Neowawraea* Rock, which has *Glochidion*-type wood, from *Drypetes*, which has *Aporusa*-type wood, and its subsequent submergence into *Flueggea* Willd., which also has *Glochidion*-type wood (Hayden & Brandt, 1984; Hayden, 1987).

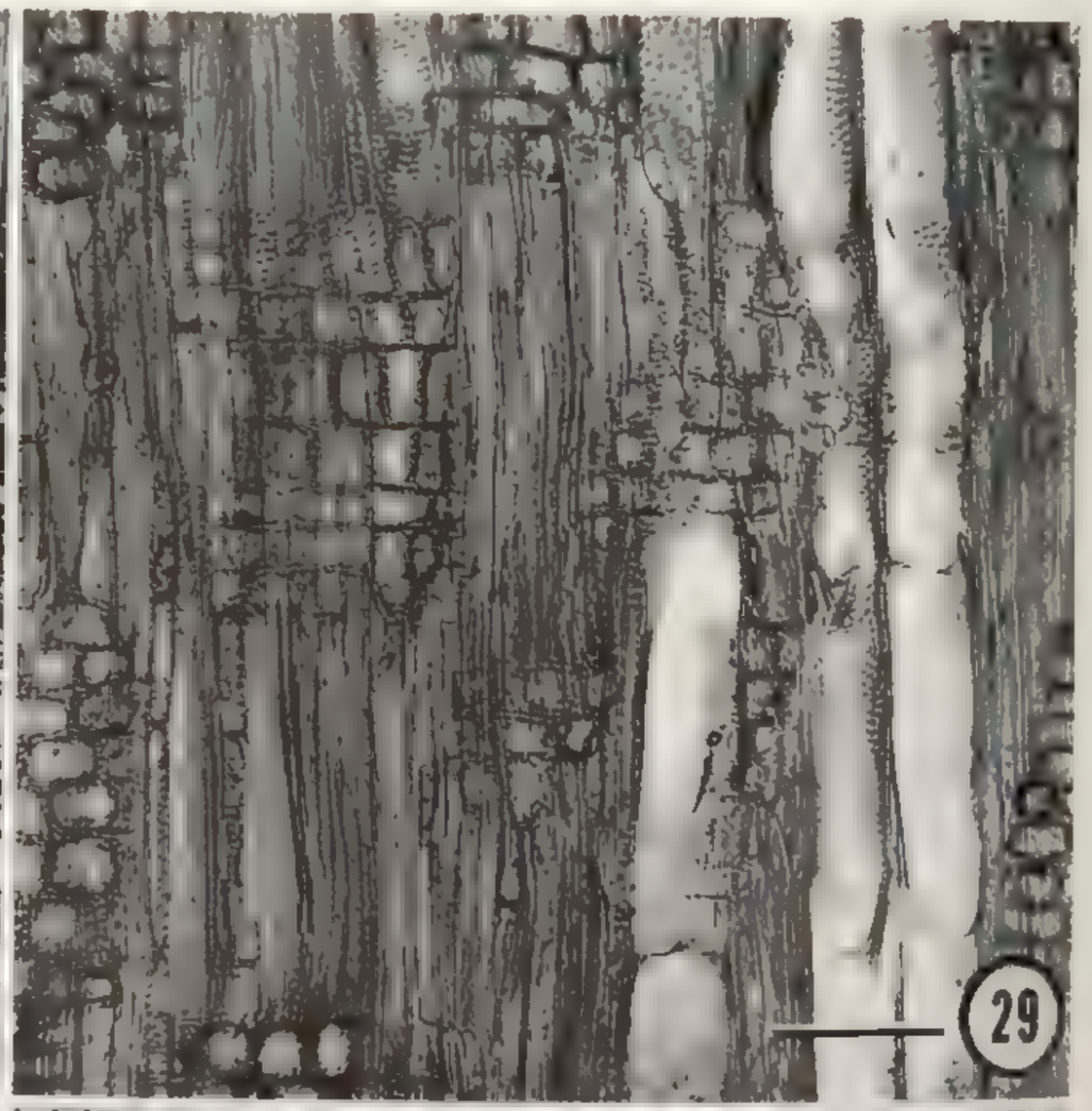
However, as wood structure of biovulate euphorbs has become better known, genera with wood that is transitional between the three categories cloud what once appeared to be a clear picture. For example, Mennega (1984) found tribal placement of *Jablonskia* Webster difficult, essentially because the wood of *Jablonskia* has an unusual combination of characters: specifically, vessel features of *Aporusa*-type woods and fiber and parenchyma features of *Glochidion*-type woods. In short, *Jablonskia* represents the reverse of the combination that characterizes most oldfieldioids. Mennega (1987) has noted additional transitional genera in her extensive survey of wood structure in Phyllanthoideae; moreover, woods of some phyllanthoids, e.g., *Lachnostylis* Turcz. and *Savia*, match the typical oldfieldioid pattern described above. Further, within Oldfieldioideae, *Podocalyx* and *Paradrypetes* possess essentially typical expressions of *Aporusa*-type structure. Clearly, the simple rubric of three wood types for biovulate euphorbs requires modification.

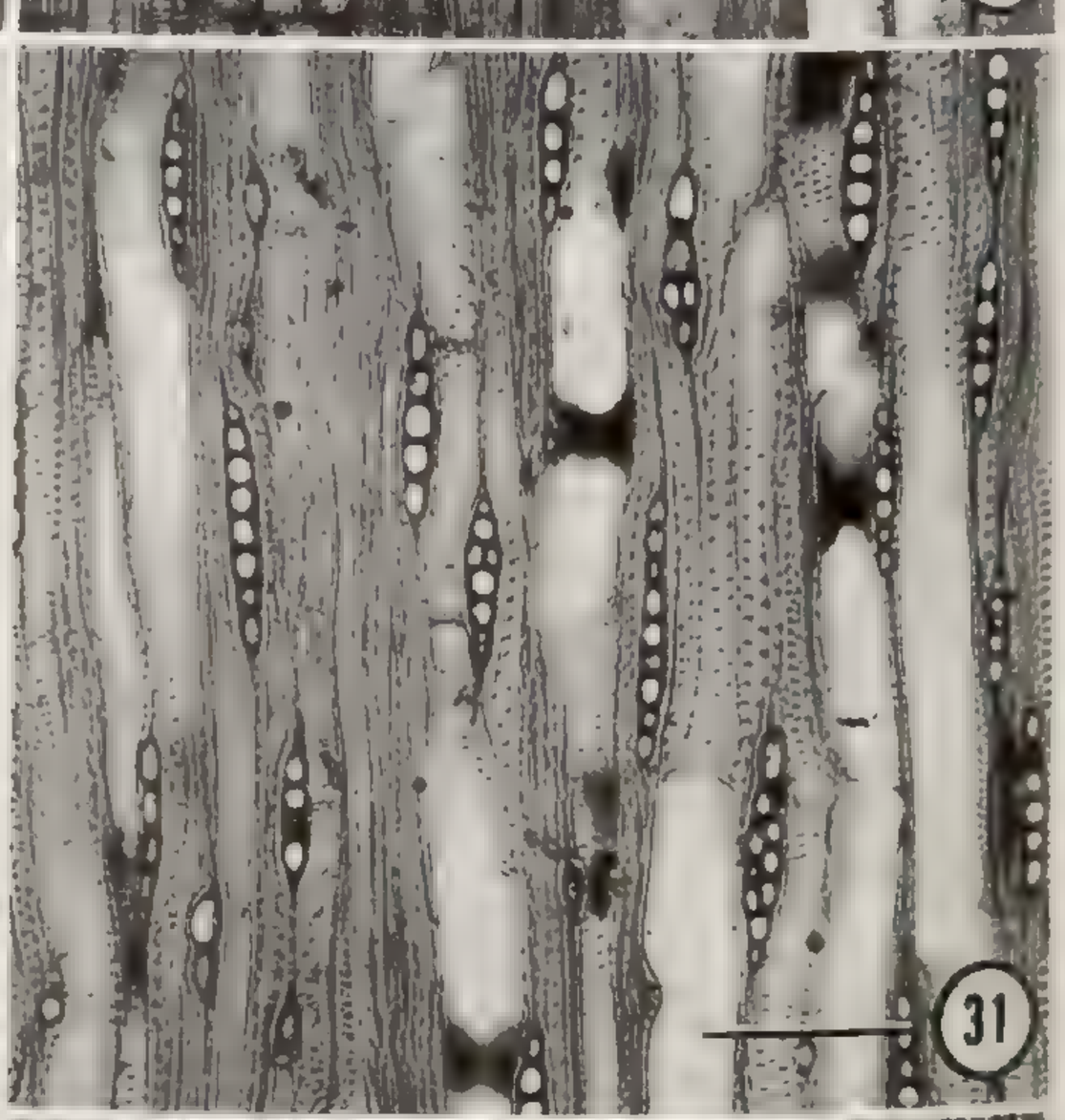
An evolutionary perspective of anatomical characters helps to clarify some of the complexity seen in woods of biovulate euphorbs. In accord with widely accepted hypotheses of wood evolution, Mennega (1987) has identified woods with long vessel elements, long scalariform perforation plates, medium to large intervascular pits, long thick-walled nonseptate fibers with bordered pits on both radial and tangential walls, and diffuse or narrowly banded axial xylem parenchyma to be primitive within Phyllanthoideae. Extant genera such as *Aporusa*, *Blotia*, and *Protomegabaria* Hutch. retain these features. Carlquist (1975) has argued convincingly that primitive vessel features are adaptive only in uniformly moist forest environments that impose minimal demands for water conduction. It may be assumed that adaptive radiation of primitive biovulate euphorbs into drier, or seasonally drier, habitats would be accompanied by evolution of more advanced vessel features. Similarly, one may reasonably suppose exploitation of nonforest and/or seasonal habitats to be associated with modification of mechanical and storage requirements of the wood; such changes would be manifest in both fiber and parenchyma features. Much of the diversity of biovulate euphorb wood structure may thus be interpreted in terms of divergence from primitive *Aporusa*-type structure, an ecologically restrictive syndrome of xylem features.

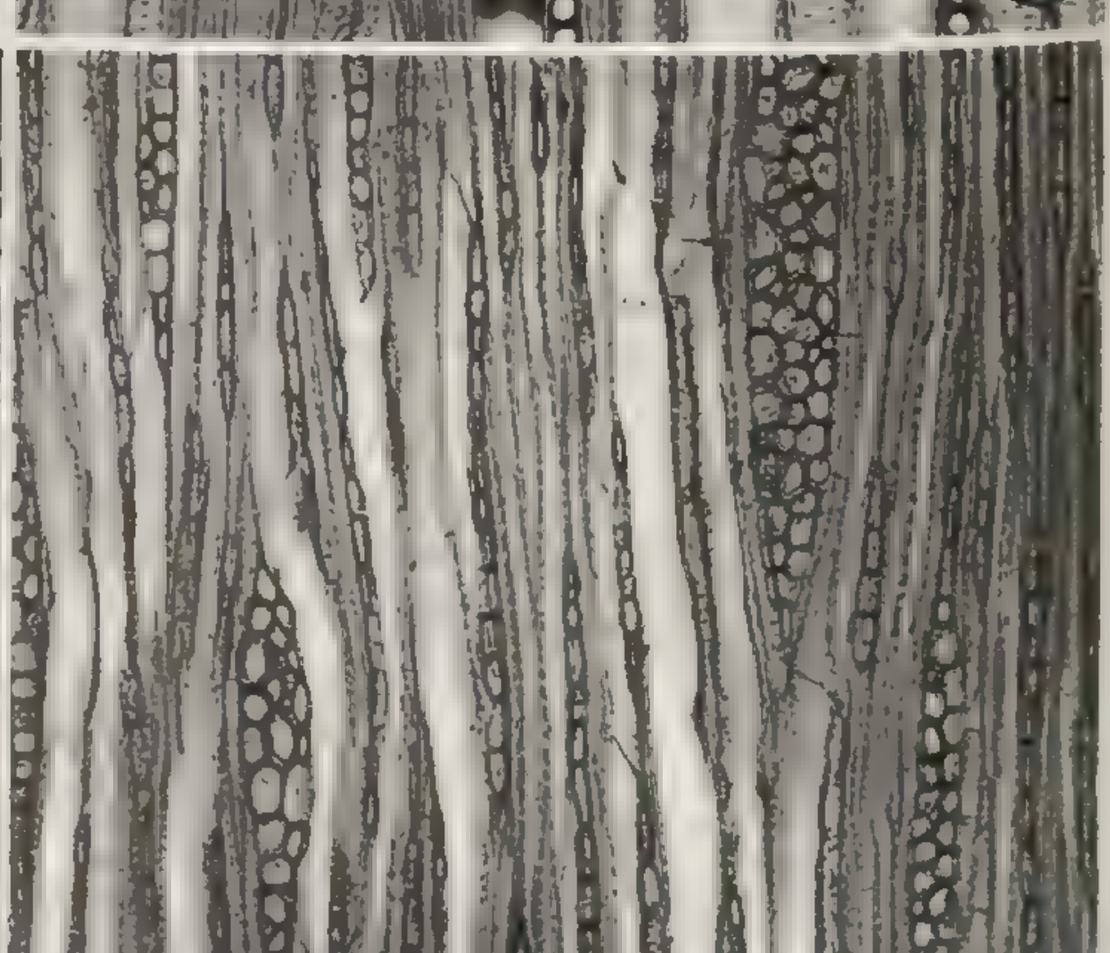
Within Phyllanthoideae, *Aporusa*- and *Glochidion*-type structure represent evolutionary extremes, but numerous transitional forms can be identified from Mennega's (1987) data. For example, tracking both perforation plates and development of septate fibers yields the following series of forms that may be viewed as intermediates between *Aporusa*- and *Glochidion*-type structure: *Actephila*, *Chascotheca* Urb., and *Pentabrachium* Muell. Arg. with exclusively scalariform perforations and some septate fibers; *Celianella* Jabl., *Didymocystis* Kuhlm., and *Jablonskia* with mixed simple and scalariform perforations and some septate fibers; *Astrocasia* Rob. & Greenm. and *Discocarpus* Klotzsch with simple perforations, but only some septate fibers. Similarly, within *Aporusa*-type woods, there is a clear transition of perforation plates from exclusively scalariform in *Aporusa*, *Heywoodia*, *Hyeronima*, *Maesobotrya* Benth., and *Putranjiva*, to mixed simple and scalariform in numerous genera and, finally, to exclusively simple in *Lachnostylis* and *Savia*. Of course, such sequences of extant genera should not be interpreted as the actual course of xylem evolution within Phyllanthoideae.

In terms of the gross vessel, fiber, and parenchyma features of Table 1, the evolutionary transformation of wood in Oldfieldioideae seems parallel to that noted for *Aporusa*-type woods. In comparison, Phyllanthoideae experienced a greater range of wood diversification with the additional development of *Glochidion*-type woods.

Within Oldfieldioideae, *Podocalyx* and *Paradrypetes* stand out as probably the most primitive woods by virtue of their very long vessel elements, multiple perforation plates, and large transitional intervascular pits; presence of perforated ray cells in these genera may also be interpreted as primitive features. Overall, their woods are comparable to primitive phyllanthoid woods with *Aporusa*-type structure. The primitive woods of *Paradrypetes* and *Podocalyx* excepted, Oldfieldioideae generally have exclusively simple perforation plates and have lost perforated ray cells, but otherwise retain the features of *Aporusa*-type structure (cf. comments on *Lachnostylis* and *Savia*, above). Much of the diversity of oldfieldioid woods is restricted largely to what are, perhaps, minor themes such as element size (Figs. 22–27), vessel grouping (Figs. 22–27), ray dimensions (Figs. 31–33), vessel-ray pitting, and parenchyma distribution (Figs. 22–27). These minor themes, however, are responsible for con-







FIGURES 28–33. Wood anatomy of Oldfieldioideae.—28. *Austrobuxus swainii* (*Symington s.n.*, *Uw 21411*), radial section, heterocellular ray and irregular slitlike vessel-ray pits.—29. *Petalostigma* sp. (*SFCw R594-2*), radial section, heterocellular rays and simple perforation plates.—30. *Podocalyx loranthoides* (*Wurdack & Adderley 42795*, *MADw 22429*), radial section, scalariform perforation plate.—31. *Androstachys johnsonii* (*Pretoria UIND 2127*, *Uw 21991*), tangential section, short and narrow rays.—32. *Celaenodendron mexicanum* (*Ortega 35*, *USw 3886*), tangential section.—33. *Tetracoccus fasciculatus* var. *fasciculatus* (*Johnston 7783*), tangential section, wide rays. All bars = 100 μm.

siderable diversity of oldfieldioid woods; based on wood features alone, it is entirely understandable that Metcalfe & Chalk (1950) sought to associate oldfieldioid genera with woods from other subfamilies.

The presence of somewhat primitive woods (*Paradrypetes* and *Podocalyx*) in Oldfieldioideae suggests that the divergence of Oldfieldioideae from Phyllanthoideae occurred quite early in the evolution of Euphorbiaceae, from ancestral stocks with relatively primitive *Aporusa*-type woods. The symplesiomorphous nature of wood features at the evolutionary transition between the subfamilies precludes the possibility of specifying one or another phyllanthoid group as closest to the origin of Oldfieldioideae based on this tissue alone.

Septate fibers, common in phyllanthoids with *Glochidion*-type structure, occur in only one oldfieldioid, *Parodiodendron*. One prominent difference, however, between this wood and the *Glochidion*-type phyllanthoids is its fairly abundant parenchyma present in initial bands, diffuse apotracheal and scanty paratracheal configurations. Typical expressions of *Glochidion*-type structure include very little parenchyma at all. The occurrence of septate fibers in *Parodiodendron* may thus represent convergence.

EVIDENCE FROM STOMATAL STRUCTURE

Configuration of the stomatal apparatus is one of the most consistent features of leaves of Oldfieldioideae. Most genera possess brachyparacytic patterns in which the subsidiary cells substantially overlie the adjacent guard cells. In this regard, Levin (1986), upon whose data much of the following is based, has shown stomatal patterns of the phyllanthoid tribes to be fairly diverse; in fact, this character provides important evidence in identifying which phyllanthoids are closest to the origin of Oldfieldioideae. As argued above, it will be necessary only to consider tribes with *Aporusa*-type wood structure. Aporuseae may be eliminated from further consideration by its consistently anisocytic stomata, a pattern never found in Oldfieldioideae. Paracytic or brachyparacytic stomata are found in the remaining tribes under consideration, i.e., Amanoeae, Antidesmeae, Drypeteae, and Wielandieae, with brachyparacytic in only Drypeteae and some Wielandieae. Subsidiary cells in *Drypetes*, like those of most Oldfieldioideae, partially overlie the adjacent guard cells. The brachyparacytic subsidiary cells of *Lachnostylis* (tribe Wielandieae) are frequently subdivided (Levin, 1986), another common character in Oldfieldioideae. Unfortunately, the distribution of stomatal characters in Phyllanthoideae and Oldfieldioideae precludes any simple statement about the point of divergence of the two subfamilies. Both characater states of three important characters (paracytic-brachyparacytic, entire-subdivided subsidiary cells, and coplanar-"piggyback" subsidiary cells) are found in both groups. This situation may be viewed as an example of Cronquist's (1988) assertion that parallel tendencies are reasonably good indicators of relationships; a rigorous cladistic analysis of Phyllanthoideae and Oldfieldioideae should distinguish the synapomorphic stomatal characters from the parallelisms.

ADDITIONAL EVIDENCE

A number of anatomical characters such as the occurrence of theoid teeth, intersecondary veins, and mucilaginous epidermis in Oldfieldioideae and primitive Phyllanthoideae are consistent with the former's derivation from the latter. Floral structure of Wielandieae is sufficiently generalized to be consistent with ancestral status. However, plesiomorphous characters such as these do not present by themselves an overly compelling case for consanguinity.

On the other hand, the often reduced carpel number and drupaceous fruits of *Drypetes* show greater (or, at least, different) specialization than that found in many Oldfieldioideae. Further, chromosome numbers of $n = 20$ for *Putranjiva* (Gill et al., 1981) and $2n = 40$ for *Drypetes* (Webster, 1967) are difficult to resolve with the counts suggesting $x = 12$ for Oldfieldioideae (see above). Extant Drypeteae are thus unsuitable as progenitors for Oldfieldioideae, but it remains conceivable that these taxa may have shared a common ancestor.

Levin & Simpson (1988) noted that the spinules and discontinuous exine foot layer in pollen of *Securinega* Comm. ex Juss. sensu stricto suggested a close relationship with Oldfieldioideae. Despite exclusively simple perforation plates, the wood of *Securinega* conforms well to the *Aporusa*-type (and thus may be out of place in tribe Phyllantheae, as pointed out by Mennega (1987)). *Securinega* also possesses paracytic stomata (Gaucher, 1902). Further anatomical data would be most useful. In our present state of ignorance, *Securinega* stands as another possible near relative to Oldfieldioideae.

SUMMARY

Taken together, stomatal and wood characters suggest that Oldfieldioideae diverged from the early differentiation of the primitive biovulate tribe Wielandieae perhaps along some of the same lines that

ultimately led to the modern genera *Drypetes* and/or *Securinega*. In a larger context, presence of theoid teeth and palmately compound leaves in Oldfieldioideae lends support to Dilleniid rather than Rosid derivation of Euphorbiaceae (cf. discussion in Levin (1986)).

Relationships within Oldfieldioideae

Classification of subfamily Oldfieldioideae has been in a state of flux over the past three decades. The following discussion focuses on anatomical data as indicators of relationships within Oldfieldioideae, specifically, the role of anatomy in modification of early classifications of Oldfieldioideae (Köhler, 1965; Webster, 1975) and the extent that anatomy supports the most recent classifications of these plants (Levin & Simpson, 1994; Webster, 1994).

Tribe Croizatieae Webster. *Croizatia*, the only genus of the tribe, is anatomically unknown.

Tribe Podocalyceae Webster. The genera associated with *Podocalyx* have undergone radical revision in the brief history of Oldfieldioideae. Köhler (1965) grouped *Podocalyx* with several genera of tribe Picrodendreae that have compound leaves plus *Tetracoccus*, whereas Webster (1975) associated it with some of the simple-leaved genera of Picrodendreae plus, again, *Tetracoccus*. As discussed below, the genera of Picrodendreae, whether bearing simple or compound leaves, form a reasonably well-defined clade and are thus better classified elsewhere. Of the two classifications presented in this volume, both link *Podocalyx* with *Paradrypetes*, albeit each in separate subtribes, but only Webster continues to include *Tetracoccus* in this tribe. There are no compelling anatomical synapomorphies that might serve to unite these three genera. The primitive wood features of *Paradrypetes* and *Podocalyx* (see above) suggest that at least these two genera are basal offshoots from the ancestral stem of Oldfieldioideae; as such, they may not be expected to share many synapomorphies with each other. Each genus of Podocalyceae bears at least one strikingly unique autapomorphy: the raphides of *Paradrypetes*, the tracheoid idioblasts of *Podocalyx*, and the ring porous wood of *Tetracoccus*.

The xeromorphic adaptations of *Tetracoccus* might just as easily obscure an early or late divergence from ancestral oldfieldioid stocks. *Tetracoccus* does share alternate vessel-ray pitting with Picrodendreae, and this character could be used to argue for its inclusion in that tribe, as classified by Levin & Simpson (1994, this volume).

Tribe Picrodendreae (Small) Webster. The genera with palmately compound leaves form the conceptual nucleus of tribe Picrodendreae. Bentham (1878) was the first to group together the biovulate euphorbs with compound leaves, associating *Oldfieldia* and *Piranhea* with the non-oldfieldioid genus *Bischofia*. Later, *Aristogeitonia* (Prain, 1912; Pax & Hoffmann, 1922, 1931) and *Celaenodendron* (Hutchinson, 1969) were added to this group, which (minus *Bischofia*) constituted subtribe Paivaeusinae of Webster (1975). (Presence of nonspiny pollen (Köhler, 1965) and *Glochidion*-type wood structure (Mennega, 1987) shows *Bischofia* to be better placed in Phyllanthoideae.) Webster (1975) maintained *Picrodendron* in a monogeneric tribe, but anatomical evidence (Hayden, 1977, 1980, see also below) suggests a close relationship among the oldfieldioid genera with compound leaves. Presently, Picrodendreae includes all oldfieldioids with compound leaves (e.g., *Stachyandra*), plus several others with unifoliolate (*Parodiodendron* and species of *Aristogeitonia*) or evidently simple leaves (*Androstachys*, *Mischodon*, and *Voatamalo*) (Levin & Simpson, 1994; Webster, 1994). Picrodendreae is characterized anatomically by alternate vessel-ray pits, bundle sheath extensions bearing crystals, well-developed areoles, and fimbrial veins at leaf margins.

Anatomical data support a subdivision of Picrodendreae that has been adopted by Levin & Simpson (1994) and Webster (1994). The first group is African–Madagascan–Sri Lankan and consists of *Androstachys*, *Aristogeitonia*, *Mischodon*, *Stachyandra*, and *Voatamalo*; these genera may be defined by stipules adnate to the petiole (Airy Shaw, 1970, 1972; Bosser, 1976; Radcliffe-Smith, 1988, 1990) and a strong tendency toward unifoliolate or simple leaves. Further, *Aristogeitonia*, *Mischodon*, and *Voatamalo* possess sclerified ray cells bearing prismatic crystals.

Mischodon was included among the genera of Dissiliariinae by Pax & Hoffman (1931) (see also Fig. 1) and Köhler (1965). I am in complete agreement with Raju (1984), who pointed out several differences in stomata and trichomes between *Mischodon* and genera of Dissiliariinae. *Mischodon* thus bears no compelling anatomical resemblance to any genus of tribe Caletieae sensu lato. Placement in Picrodendreae is definitely superior to any previous classification of the genus, a conclusion confirming, to some extent, suggestions made by Airy Shaw (1972) based on the similarity of stipules of *Aristogeitonia* and *Mischodon*.

The second subgroup of Picrodendreae is neotropical and consists of *Celaenodendron*, *Picro-*

dendron, and *Piranhea*; these genera are uniformly trifoliolate, have alternate phyllotaxy, and lack the epidermal mucilage which is so widespread in the family. *Parodiodendron*, also neotropical, presents an interesting situation. It shares with the trifoliolate genera alternate phyllotaxy and unusually large (for Oldfieldioideae) intervascular pits; but its leaves are unifoliolate and lack the fimbrial vein characteristic of all other members of the tribe. Further, *Parodiodendron* is unique within the subfamily by virtue of its septate wood fibers. Nevertheless, *Parodiodendron* seems best accommodated among the other neotropical Picrodendreae, especially if its discordant features are viewed as autapomorphies.

Oldfieldia is not included in either of the above groups. Anatomically, its trichomes and presence (in some species) of homocellular procumbent rays resemble these features in the otherwise rather different genera *Androstachys* and *Stachyandra*. *Oldfieldia* may represent a relictual element derived early from the ancestors to Picrodendreae prior to its differentiation into otherwise distinct New and Old World lineages.

Levin & Simpson (1994) include *Tetracoccus* in Picrodendreae, but aside from the alternate vessel-ray pits of these desert shrubs there is no compelling anatomical support for this placement.

Tribe Caletieae Muell. Arg. With virtually no contrary opinion on record, *Micrantheum*, *Pseudanthus*, and *Stachystemon* have been recognized as close relatives for well over a century (Agardh, 1858; Mueller, 1866; Bentham, 1880; Grüning, 1913; Pax & Hoffmann, 1931; Hutchinson, 1969). These shrubby xerophytes of Australia constitute the traditional circumscription of Tribe Caletieae. Their gross similarity and narrow "Stenolobeae"-type cotyledons precluded serious comparison with other euphorbs prior to the utilization of pollen characters in the systematics of Euphorbiaceae. *Neoroepera* was added to what was then a wholly Australian tribe by Webster (1975) who was impressed, no doubt, by the numerous scattered apertures (Punt, 1962; Köhler, 1965) shared by all four genera. Additional palynological and anatomical studies have refined concepts of relationships to the extent that, now, all Australasian genera except *Mischodon* are perceived to constitute a single clade, the greatly expanded Tribe Caletieae sensu lato (Levin & Simpson, 1994; Webster, 1994).

The presence of crenulate "piggyback" subsidiary cells is a particularly striking synapomorphy linking all Australasian genera of Oldfieldioideae, plus the monotypic *Hyaenanche*, endemic to the western Cape of South Africa. *Hyaenanche* has no other obvious close relatives within Oldfieldioideae. Anatomically, its marginal venation is remarkable, but, apparently, autapomorphic. It is perhaps best viewed as a remnant of the Australasian stem of the subfamily, from which it has been separated since the breakup of Gondwanaland. Placement of *Hyaenanche* in a separate monogeneric subtribe seems appropriate.

Hyaenanche excluded, all other members of Tribe Caletieae share another epidermal feature, longitudinally chambered cells that bear copious mucilage deposits in their lower halves. Taken together, crenulate subsidiary cells and mucilaginous epidermis provide a robust definition of the Australasian clade. The Australasian genera also tend to have relatively low rank foliar venation and poorly defined areoles, but it seems these vein features are best interpreted as plesiomorphic. The distinctive epidermal features of Caletieae sensu lato are found in *Scagea*, which argues strongly for its placement here and not in Acalyphoideae or Crotonoideae as suggested by McPherson (1985); the uniovulate carpels of *Scagea* may thus be homoplasious with Acalyphoideae, Crotonoideae, and Euphorbioideae.

Both Webster (1994) and Levin & Simpson (1994) divide the Australasian oldfieldioids into three subtribes, Dissiliariinae, Petalostigmatinae, and Pseudanthinae.

Aside from the epidermal characters that define the entire Australasian clade of Oldfieldioideae, the genera of subtribe Dissiliariinae share few phylogenetically significant anatomical structures. Woods of Dissiliariinae have irregular vessel-ray pits (Fig. 28), but this is probably a plesiomorphic feature in the subfamily. Leaf margins tend to be entire in Oldfieldioideae, but, as noted above, exceptional toothed leaves occur in species of *Austrobuxus*, *Choriceras*, and *Dissiliaria*, and this feature, too, is probably plesiomorphic. *Austrobuxus*, with a preponderance of solitary pores, long vessel elements (often >1 mm), occasional scalariform perforations, and abundant tracheids, seems to be the least specialized genus of the subtribe in terms of wood anatomy. Anatomically, *Dissiliaria* stands apart from the remainder of its tribe by virtue of high rank venation, well-developed and somewhat oriented areoles, narrow ultimate tracheids in veinlets, fimbrial veins, wavy anticlinal walls of leaf epidermis cells, bundle sheath extensions, and libriform wood fibers.

Whyanbeelia lacks crystal-bearing axial xylem parenchyma; in this respect it resembles wood of *Petalostigma* and Pseudanthinae; its retention in

Dissiliariinae may be challenged on this character. Lack of wood material precludes determining whether *Scagea* and *Kairothamnus* are better included in Dissiliariinae (crystalliferous axial xylem parenchyma present) or either Petalostigmatinae or Pseudanthinae (said crystals absent); pollen suggests relationship with Pseudanthinae (Levin & Simpson, 1994). Subtribe Dissiliariinae appears to be a paraphyletic assemblage at the base of the Australasian clade.

Petalostigma is a distinctive genus of Australia and southern New Guinea characterized, as its name suggests, by broad petaloid stigmas. The presence of crenulate subsidiary cells and chambered epidermal cells with mucilage shows the association of *Petalostigma* with Australasian genera of Oldfieldioideae to be superior to its former association with *Androstachys* (Webster, 1975; Hayden, 1982); this realignment is also supported biogeographically.

Both Levin & Simpson (1994) and Webster (1994) place *Petalostigma* in its own monogeneric tribe, evidently because its pollen bears at least some apertures out of the equatorial plane (Punt, 1962; Köhler, 1965), thus differing from the pollen of Pseudanthinae. Nevertheless, *Petalostigma* shares some anatomical features with Pseudanthinae: lack of crystalliferous axial xylem parenchyma and the presence of nonlignified phloem fibers in foliar veins. In *Petalostigma* the phloem fibers are thin-walled, whereas in Pseudanthinae the walls are so thick that lumina are almost completely occluded, so the similarity is only partial in this regard.

From the numerous comments above in the anatomical descriptions, it is clear that the four Australian genera of subtribe Pseudanthinae (i.e., tribe Caletieae in the traditional or narrow sense) are united by a suite of characters involving leaf architecture, leaf anatomy, and wood structure (see also Hayden, 1981). Many of the anatomical characters of these genera suggest a sequence of increasing xeromorphy involving general reduction of leaf size, increasing disorganization of the venation, and increasing prominence of a massive sclerenchymatous marginal vein. *Neoroepera* is particularly interesting in that *N. buxifolia* Muell. Arg. is similar to Dissiliariinae in some characters (incomplete marginal ultimate venation and lignified phloem fibers in foliar veins), whereas *N. banksii* Benth. conforms with other Pseudantheae (massive intramarginal vein and unlignified phloem fibers). Radcliffe-Smith's (1993) inclusion of *Stachystemon* within *Pseudanthus* increases the diversity of venation patterns in the latter, but otherwise these taxa are quite similar anatomically and evidently very closely related. Levin & Simpson (1994) provide further discussion of the relationships of *Kairothamnus*, *Neoroepera*, *Petalostigma*, and *Scagea* with the other genera of Pseudanthinae.

Literature Cited

Agardh, J. G. 1858. Theoria Systematis Plantarum ... C. W. K. Gleerup, Lund.

Airy Shaw, H. K. 1965. Diagnoses of new families, new names, etc., for the seventh edition of Willis's "Dictionary." Kew Bull. 18: 249–273.

———. 1966. A Dictionary of the Flowering Plants and Ferns, Ed. 7. Univ. Press, Cambridge.

———. 1970. The genus *Androstachys* Prain in Africa. Adansonia, ser. 2 10: 519–524.

———. 1972. A second species of the genus *Aristogeitonia* Prain (Euphorbiaceae), from East Africa. Kew Bull. 26: 495–498.

———. 1973. A Dictionary of the Flowering Plants and Ferns, Ed. 8. Univ. Press, Cambridge.

———. 1975. The Euphorbiaceae of Borneo. Kew Bull. Additional Series IV. Her Majesty's Stationery Office, London.

———. 1976. New or noteworthy Australian Euphorbiaceae. Kew Bull. 31: 341–398.

———. 1980a. New Euphorbiaceae from New Guinea. Kew Bull. 34: 591–598.

———. 1980b. The Euphorbiaceae of New Guinea. Kew Bull. Additional Series VIII. Her Majesty's Stationery Office, London.

———. 1983. Euphorbiaceae. Pp. 129–135 *in* B. D. Morley & H. R. Tolken (editors), Flowering Plants in Australia. Rigby Publishers, Adelaide.

Alvin, K. L. 1987. Leaf anatomy of *Androstachys johnsonii* Prain and its functional significance. Ann. Bot. 59: 579–591.

——— & T. A. Rao. 1987. On the unusual distribution pattern of leaf sclereids in *Androstachys johnsonii* Prain (Euphorbiaceae). Bot. J. Linn. Soc. 95: 55–60.

Anonymous. 1909. Makruss or Zimbiti. Bull. Misc. Inform. 1909: 201–204. [Probably attributable to D. Prain & L. A. Boodle.]

Araujo, P. A. M. & A. Mattos Filho. 1984. Estrutura das madeiras brasileiras de dicotiledôneas. XXVI. Euphorbiaceae. Rodriguésia 36: 25–40.

Assailly, A. 1954. Contribution à la détermination des Euphorbiacées par la méthode anatomique. Bull. Soc. Hist. Nat. Toulouse 89: 157–194.

Bailey, I. W. 1936. The problem of differentiating and classifying tracheids, fiber-tracheids, and libriform wood fibers. Trop. Woods 45: 18–23.

Baillon, H. 1858. Etude générale du groupe des Euphorbiacées. Victor Masson, Paris.

———. 1878. Euphorbiaceae. The Natural History of Plants. 5: 105–256. L. Reeve, London.

Bamber, R. K. 1974. Fibre types in the wood of Euphorbiaceae. Austral. J. Bot. 22: 629–634.

Bentham, G. 1878. Notes on Euphorbiaceae. J. Linn. Soc., Bot. 17: 185–267.

———. 1880. Euphorbiaceae. *In*: G. Bentham & J. D. Hooker (editors), Genera Plantarum. 3: 239–340. L. Reeve, London.

Bolza, E. & W. G. Keating. 1972. African Timbers—The Properties and Characteristics of 700 Species. Division of Building Research, Commonwealth Scientific and Industrial Research Organization, Melbourne.

Bosser, J. 1976. *Voatamalo*, nouveau genre d'Euphorbiaceae de Madagascar. Adansonia 15: 333–340.

Carlquist, S. 1975. Ecological Strategies of Xylem Evolution. Univ. California Press, Berkeley.

Cronquist, A. 1988. Evolution and Classification of Flowering Plants, 2nd ed. New York Botanical Garden, New York.

Dahlgren, R. & A. E. van Wyk. 1988. Structures and relationships of families endemic to or centered in southern Africa. Monogr. Syst. Bot. Missouri Bot. Gard. 25: 1–94.

Dehay, C. 1935. L'appareil libéro-ligneux foliare des Euphorbiacées. Ann. Sci. Nat. Bot. 17: 147–296.

Endlicher, S. 1836–1840. Genera Plantarum Secundum Ordines Naturales Disposita. Fr. Beck, Vienna.

Fritsch, R. 1972. Chromosomenzahlen von pflanzen der insel Kuba. II. Kulturpflanze 19: 305–313.

Froembling, W. 1896. Anatomisch-systematische Untersuchung von Blatt und Axe der Crotoneen und Euphyllantheen. Bot. Centralbl. 65: 129–139, 177–192, 241–249, 289–297, 321–329, 369–378, 403–411, 433–442, pls. 1–2.

Gamble, J. S. 1922. A Manual of Indian Timbers. Reprint of ed. 2. Sampson, Low, Marston & Co., London.

Gaucher, L. 1902. Recherches anatomiques sur les Euphorbiacées. Ann. Sci. Nat. Bot, Sér. 8, 15: 161–309.

Gill, B. S., S. S. Bir & Y. S. Bedi. 1981. Cytological studies on woody Euphorbiaceae from north and central India. New Botanist 8: 35–44.

Giraud, B. 1983. Les cellules perforées des rayons ligneux chez les Euphorbiacées. Bull. Mus. Natl. Hist. Nat. (Paris) sér. 4, sect. B, Adansonia 5: 213–221.

Gruning, G. 1913. Euphorbiaceae–Porantheroideae et Ricinocarpoideae. Das Pflanzenreich IV. 147(Heft 58): 1–97.

Hakki, M. I. 1985. Studies on West Indian plants. 3. On floral morphology, anatomy, and relationship of *Picrodendron baccatum* (L.) Krug & Urban (Euphorbiaceae). Bot. Jahrb. Syst. 107: 379–394.

Hans, A. S. 1973. Chromosomal conspectus of the Euphorbiaceae. Taxon 22: 591–636.

Hassall, D. C. 1976. Numerical and cytotaxonomic evidence for generic delimitation in Australian Euphorbieae. Austral. J. Bot. 24: 633 640.

Hayden, W. J. 1977. Comparative anatomy and systematics of *Picrodendron, genus incertae sedis*. J. Arnold Arbor. 58: 257–279.

———. 1980. Systematic Anatomy of Oldfieldioideae (Euphorbiaceae). Ph.D. Dissertation (unpublished). University of Maryland, College Park.

———. 1981. Systematic anatomy of Caletieae (Euphorbiaceae–Oldfieldioideae). Bot. Soc. Amer. Misc. Ser. Publ. No. 160: 69. [Abstract.]

———. 1982. Comparative anatomy and relationships of *Androstachys* Prain and *Petalostigma* F. v. Mueller (Euphorbiaceae subfam. Oldfieldioideae). Bot. Soc. Amer. Misc. Ser. Publ. No. 162: 96. [Abstract.]

———. 1987. The identity of the genus *Neowawraea* (Euphorbiaceae). Brittonia 39: 268–277.

——— & D. S. Brandt. 1984. Wood anatomy and relationships of *Neowawraea* (Euphorbiaceae). Syst. Bot. 9: 458–466.

———, W. T. Gillis, D. E. Stone, C. R. Broome & G. L. Webster. 1984. Systematics and palynology of *Picrodendron*: Further evidence for relationship with the Oldfieldioideae (Euphorbiaceae). J. Arnold Arbor. 65: 105–127.

Heimsch, C., Jr. 1942. Comparative anatomy of the secondary xylem in the "Gruinales" and "Terebinthales" of Wettstein with reference to taxonomic grouping. Lilloa 8: 82–198.

Hickey, L. J. & J. A. Wolfe. 1975. The bases of angiosperm phylogeny: Vegetative morphology. Ann. Missouri Bot. Gard. 62: 538–589.

Hunziker, A. T. 1969. *Parodiodendron* gen. nov.: Un nuevo genero de Euphorbiaceae (Oldfieldioideae) del noroeste Argentino. Kurtziana 5: 329–341.

Hurusawa, I. 1954. Eine nochmalige Durchsicht des herkömlichen Systems der Euphorbiaceen im weiteren Sinne. J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 6: 209–342.

Hutchinson, J. 1969. Tribalism in the family Euphorbiaceae. Amer. J. Bot. 56: 738–758.

Jussieu, A. de. 1824. De Euphorbiacearum generibus medisque earumdem viribus tentamen, . . . Didot, Paris.

Köhler, E. 1965. Die Pollenmorphologie der Biovulaten Euphorbiaceae und ihre Bedeutung für die Taxonomie. Grana Palynol. 6: 26–120.

Lebacq, L. & R. Dechamps. 1964. Essais d'identification anatomique des bois de l'Afrique Centrale. Musée Royal de l'Afrique Centrale, Tervuren.

Levin, G. A. 1986. Systematic foliar morphology of Phyllanthoideae (Euphorbiaceae). I. Conspectus. Ann. Missouri Bot. Gard. 73: 29–85.

———. 1992. Systematics of *Paradrypetes* (Euphorbiaceae). Syst. Bot. 17: 74–83.

——— & M. G. Simpson. 1988. Taxonomic implications of pollen ultrastructure in the Phyllanthoideae and Oldfieldioideae (Euphorbiaceae). Amer. J. Bot. 75(6, part 2): 189–190. [Abstract.]

——— & ———. 1994. Phylogenetic implications of pollen ultrastructure in the Oldfieldioideae (Euphorbiaceae). Ann. Missouri Bot. Gard. 81: 203–238.

Mathou, T. 1940. Recherches sur la famille des Buxacées. Trav. Lab. Bot. Fac. Méd. & Pharmacol. Univ. Toulouse 1940: 130–136.

McPherson, G. 1985. *Scagea*, a new genus of Euphorbiaceae from New Caledonia. Bull. Mus. Natl. Hist. Nat., B, Adansonia 3: 247–250.

Mennega, A. M. W. 1984. Wood structure of *Jablonskia congesta* (Euphorbiaceae). Syst. Bot. 9: 236–239.

———. 1987. Wood anatomy of the Euphorbiaceae, in particular of the subfamily Phyllanthoideae. Bot. J. Linn. Soc. 94: 111–126.

Metcalfe, C. R. & L. Chalk. 1950. Anatomy of the Dicotyledons. Clarendon Press, Oxford.

Milanez, F. R. 1935. Anatomie de *Paradrypetes ilicifolia*. Arq. Inst. Biol. Veg. 2: 133–156.

Mueller, J. (Mueller Arg.). 1866. Euphorbiaceae. *In:* A. de Candolle (editor), Prodromus systematis naturalis regni vegetabilis. 15(2): 189–1286. Fortin Masson, Paris.

Nazma, B. Sundarsivarao & R. Vijendrarao. 1981.

Occurrence of perforated ray cells in the wood of *Drypetes roxburghii* (Wall.) Hurusawa. I.A.W.A. Bull., n.s. 2: 201–203.

PAX, F. 1884. Anatomie der Euphorbiaceen. Bot. Jahrb. Syst. 5: 384–421.

———. 1890. Euphorbiaceae. *In:* A. Engler & K. Prantl (editors), Die Natürlichen Pflanzenfamilien. Ed. 1. Teil III. Abteilung 5: 1–119. Wilhelm Engelmann, Leipzig.

———. 1925. Die Phylogenie der Euphorbiaceae. Bot. Jahrb. Syst. 59: 9–182.

——— & K. HOFFMANN. 1922. Euphorbiaceae–Phyllanthoideae–Phyllantheae. Das Pflanzenreich IV. 147-XV (Heft 81): 1–349.

——— & K. HOFFMANN. 1931. Euphorbiaceae. *In:* A. Engler & K. Prantl, Die Natürlichen Pflanzenfamilien. Ed. 2. 19c: 11–253. Wilhelm Engelmann, Leipzig.

PRAIN, D. 1912. *Aristogeitonia*. Pp. 625–626 *in* W. T. Thiselton-Dyer (editor), Flora of Tropical Africa, Vol. 6, sect. 1. L. Reeve, London.

PUNT, W. 1962. Pollen morphology of the Euphorbiaceae with special reference to taxonomy. Wentia 7: 1–116.

PYYKKO, M. 1979. Morphology and anatomy of leaves from some woody plants in a humid tropical forest of Venezuelan Guayana. Acta Bot. Fenn. 112: 1–41.

RADCLIFFE-SMITH, A. 1988. Notes on Madagascan Euphorbiaceae I. On the identity of *Paragelonium* and on the affinities of *Benoistia* and *Claoxylopsis*. Kew Bull. 43: 625–647.

———. 1990. Notes on Madagascan Euphorbiaceae. III. *Stachyandra*. Kew Bull. 45: 561–568.

———. 1993. Notes on Australian Euphorbiaceae II: *Pseudanthus* and *Stachystemon*. Kew Bull. 42: 165–168.

RAJU, V. S. 1984. Notes on *Mischodon zeylanicus* Thwaites: A little-known euphorbiaceous plant from Sri Lanka and southern India. J. Econ. Taxon. Bot. 5: 165–167.

——— & P. N. RAO. 1977. Variation in the structure and development of foliar stomata in the Euphorbiaceae. Bot. J. Linn. Soc. 75: 69–97.

RAO, P. N. & V. S. RAJU. 1985. Foliar trichomes in the family Euphorbiaceae. Pp. 128–136 *in* C. M. Govil & V. Kumar (editors), Trends in Plant Research. Bishen Singh & Mahendra Pal Singh, Dehra Dun.

RECORD, S. J. 1928. The "palo prieto" of west central Mexico. Trop. Woods 14: 8–12.

———. 1938. The American woods of the family Euphorbiaceae. Trop. Woods 54: 7–40.

——— & R. W. HESS. 1943. Timbers of the New World. Yale Univ. Press, New Haven.

ROTH, I. 1981. Structural patterns of tropical barks. *In:* Encyclopedia of Plant Anatomy, Volume 9, Part 3. Borntraeger, Berlin.

ROTHDAUSCHER, H. 1896. Ueber die anatomischen Verhältnisse von Blatt und Axe der Phyllantheen (mit Ausschluss der Euphyllantheen). Bot. Centralbl. 68: 65–79, 97–108, 129–136, 161–169, 193–203, 248–253, 280–285, 305–315, 338–346, 385–393.

SARKAR, A. K. & N. DATTA. 1980. Cytological assessment of the family Euphorbiaceae. II. Tribe Phyllantheae. Proc. Indian Sci. Congr. Assoc. (III, C) 67: 48–49.

SOLEREDER, H. 1908. Systematic Anatomy of the Dicotyledons. (Translated by L. A. Boodle & F. E. Fritsch; revised by D. H. Scott.) Clarendon Press, Oxford.

STERN, W. L. 1988. Index xylariorum. 3. Institutional wood collections of the world. IAWA Bull. n.s. 9: 203–252.

STONE, H. 1904. The Timbers of Commerce and Their Identification. William Rider & Son, London.

WEBSTER, 1967. The genera of Euphorbiaceae in the southeastern United States. J. Arnold Arbor. 48: 303–430.

———. 1975. Conspectus of a new classification of the Euphorbiaceae. Taxon 24: 593–601.

———. 1987. The saga of the spurges: A review of classification and relationships in the Euphorbiales. Bot. J. Linn. Soc. 94: 3–46.

———. 1994. Synopsis of the genera and suprageneric taxa of Euphorbiaceae. Ann. Missouri Bot. Gard. 81: 33–144.

——— & K. I. MILLER. 1963. The genus *Reverchonia* (Euphorbiaceae). Rhodora 65: 193–207.

———, L. GILLESPIE & J. STEYERMARK. 1987. Systematics of *Croizatia* (Euphorbiaceae). Syst. Bot. 12: 1–8.

WORBES, M. 1989. Growth rings, increment and age of trees in inundation forests, savannas and a mountain forest in the Neotropics. IAWA Bull. n.s. 10: 109–122.

APPENDIX 1. Specimens of Oldfieldioideae examined. Xylarium acronyms follow Stern (1988).

Androstachys johnsonii Prain. Leaf: *Gomes & Sousa 2202* (K); *Wellcome Chemical Research Laboratory s.n.* (K). Wood: *Capuron 3594.R.4*, USw 27434 (= CTFw 13817) (TAN); DDw 2385; *Pardy s.n.*, USw 21255 (= Uw 14606); *Pretoria UIND 2127*, Uw 21991; PRFw 20686.

Aristogeitonia monophylla Airy Shaw. Leaf: *Bally & Smith B 14376* (K). Woody twig: *Tanner 3386* (K).

Aristogeitonia sp. *Begue 727.R.1*, CTFw 13770 (TAN).

Austrobuxus brevipes Airy Shaw. Leaf: *Stauffer & Blanchon 5751* (K). Wood: *McPherson 4579* (MO).

Austrobuxus carunculatus (Baill.) Airy Shaw. Leaf: *Baumann-Bodenheim 16087* (US).

Austrobuxus clusiaceus (Baill.) Airy Shaw. Leaf: *McKee 2570* (US); *Webster 14972* (DAV). Woody twig: *Webster 14972* (DAV).

Austrobuxus cuneatus (Airy Shaw) Airy Shaw. Leaf: *McKee 12184* (K).

Austrobuxus eugeniifolius (Guillaum.) Airy Shaw. Leaf: *Guillaumin & Baumann-Bodenheim 12908* (US); *Hürlimann 1331* (US).

Austrobuxus horneanus (A. C. Smith) Airy Shaw. Leaf: *A. C. Smith 6669* (US). Wood: *A. C. Smith 6872*, Aw 28453 (= USw 30522), (A, US).

Austrobuxus huerlimannii Airy Shaw. Leaf: *McKee 4850* (K).

Austrobuxus lugubris Airy Shaw. Leaf: *McKee 25773* (K).

Austrobuxus montanus (Ridl.) Airy Shaw. Leaf: *Wray & Robinson 5424* (K).

Austrobuxus nitidus Miq. Leaf: *Chew & Corner RSNB 4107* (US); *Chew & Corner RSNB 4608* (US). Wood: FPAw DFP 30239; PRFw 21393 (SAR); PRFw 21395 (SAR); *Si Boecca 7983*, USw 29100 (MICH); *Sy-*

mington s.n., Uw 21411 (= KEPw 3602) (KEP); USw 30796, Uw 14635, (= SARFw 13234) (SAR).

Austrobuxus ovalis Airy Shaw. Leaf: *McKee 26894* (K).

Austrobuxus pauciflorus Airy Shaw. Leaf: *Baumann-Bodenheim 14113* (K); *McPherson 3935* (MO). Wood: *McPherson 3923* (MO); *McPherson 3935* (MO); *McPherson 4603* (MO).

Austrobuxus rubiginosus (Guillaum.) Airy Shaw. Leaf: *Baumann-Bodenheim 15010* (US); *Hürlimann 1486* (US).

Austrobuxus swainii (de Beuzev. & C. T. White) Airy Shaw. Leaf: *Boorman s.n.* (NSW); *Hewitt s.n.* (NSW); *Johnson & Constable s.n.* (NSW). Wood: *de Beuzeville s.n.*, MADw 10449 (= FPAw DFP 8606).

Austrobuxus vieillardii (Guillaum.) Airy Shaw. Leaf: *Schmid 2514* (K). Wood: *McKee 25222*, FPAw DFP 33881 (K).

Austrobuxus sp. Leaf: *University of California, Davis Greenhouse B73.173.* Wood: *Hyland 6918* (DAV); *Webster & Hyland 18927* (DAV).

Celaenodendron mexicanum Standley. Leaf: *Ortega 4962* (US); *Ortega 6367* (US). Wood: *Ortega 35*, USw 3886 (= Aw 4494, MADw 29901, MAD-SJRw 1200); *Ortega 6367* (US); Uw 21735 (= Aw 30657).

Choriceras tricorne (Benth.) Airy Shaw. Leaf: *Forman s.n.* (LAE, US). Wood: *Pullen 7135*, MADw 29097, FPAw-Pullen 7135 (A, CANB, K, L, LAE).

Dissiliaria baloghioides F. v. Muell. Leaf: *Bailey s.n.* (US); *Francis & White s.n.* (US). Wood: *Bailey's Queensland Woods 366*, Aw 26736; PRFw 28015; USw 32037, Uw 14625 (= FPAw DFP 3127).

Hyaenanche globosa (Gaertn.) Lam. Leaf: *Bayliss BSBRI 576* (US); *Godfrey SH-1257* (US); *Werderman & Oberdieck 528* (US). Wood: *Böhmer & Verdoucq s.n.* (PRE); *Botanical Research Institute Pretoria s.n.* (PRE); *Werderman & Oberdieck 528* (US).

Kairothamnus phyllanthoides (Airy Shaw) Airy Shaw. Leaf: *Johns NGF 47324* (K); *Streimann NGF 45108* (K).

Longetia buxoides (Baill.) Airy Shaw. Leaf: *Baumann-Bodenheim 5605* (US). Wood: *Baumann-Bodenheim 5605* (US).

Micrantheum demissum F. v. Muell. Leaf: *Hunt 2802* (US). Woody twig: *Hunt 2802* (US).

Micrantheum ericoides Desf. Leaf: *Hotchkiss 428* (US); *Johnson & Constable 19095* (US). Woody twig: *Cambage 495* (NSW).

Micrantheum hexandrum Hook. f. Leaf: *Boorman s.n.* (US); *McGillivray 3196* (DAV); *Schodde 1177* (US). Woody twig: *Boorman s.n.* (US); *Whaite & Whaite 3536* (NSW).

Mischodon zeylanicus Thwaites. Leaf: *Ripley 05* (US); *Wheeler 12079* (US). Wood: *Jayasuriya 2434* (PDA); *Wheeler 12079* (US).

Neoroepera banksii Benth. Leaf: *Banks & Solander s.n.* (US). Woody twig: *Horner & Taylor s.n.* (NSW).

Neoroepera buxifolia White. Leaf: *White 12095* (US). Woody twig: *White 12095* (US).

Oldfieldia africana Benth. & Hook. f. Leaf: *Cooper 88* (K, MAD, US); *Cooper 439* (US). Wood: *Commercial sample*, USw 19900; *Cooper 88*, USw 4517, Uw 14636 (= Aw 16930, MADw 30131, MAD-SJRw 13738) (K, MAD, US); *Cooper 111*, USw 4538, (= Aw 16931, MADw 30132, MAD-SJRw 13761) (K, MAD); *Cooper 295*, USw 4882, (= Aw 16932, MAD-SJRw 15207) (MAD).

Oldfieldia dactylophylla (Welw. ex Oliv.) Léonard. Wood: *Cons. For. Tanganyika Territory 254*, Uw 10951 (PRFw 13495).

Oldfieldia macrocarpa Léonard. Wood: *Dechamps (Comité Nat. du Kivu) s.n.*, TERVw 1605 (BR).

Oldfieldia somalensis (Chiov.) Milne-Redhead. Leaf: *Perdue & Kibuwa 10005* (NA). Wood: *Schlieben 6371 (wood no. 558)*, Uw 15635 (= MAD-SJRw 34030).

Oldfieldia sp. Wood: *Dechamps 330*, TERVw 7522; *Dechamps 335*, TERVw 7527; *Dechamps 655*, TERVw 8499 (BR).

Parodiodendron marginivillosum (Speg.) Hunziker. Leaf: *Hueck 469* (US). Wood: *Vervoorst & Cuezzo 7.610C* (LIL).

Petalostigma banksii Britten & S. Moore. Leaf: *Perry 1981* (US); *Perry 3531* (US); *Perry 3562* (US). Wood: *Doherty s.n.*, USw 21280.

Petalostigma "glabrescens" (probably referable to *P. pubescens* or *P. triloculare*). Leaf: *Clemens 42580* (US); *Wilson 679* (US). Wood: SFCw R 594-2.

Petalostigma pubescens Domin. Leaf: *White 12421* (US). Wood: SFCw R 594-3; SFCw R 977-256; *White s.n.*, PRFw 17591.

Petalostigma quadriloculare F. v. Muell. Leaf: *Clemens 42561* (US); *Lazarides 6669* (US). Wood: PRFw 2921; PRFw 24259, (= Uw 10949); PRFw 10913, (= Uw 10948); *Webster & Hyland 18879* (DAV).

Piranhea longepedunculata Jablonski. Leaf: *Breteler 4969* (US). Wood: *Breteler 4970*, MAD-SJRw 55650, (= Uw 12254) (MER, US); *Breteler 5096*, USw 35682, (= Uw 12306, MAD-SJRw 55702) (MER, NY, U, US, WAG).

Piranhea trifoliata Baill. Leaf: *Krukoff 5924* (US); *Steyermark 86615* (US). Wood: *Capucho 493*, USw 22377 (= Aw 4526, MADw 30166, MAD-SJRw 23457) (F, IAN); *Ducke s.n.*, USw 31485 (MAD); *Krukoff 6163*, USw 7524 (US).

Podocalyx loranthoides Klotzsch. Leaf: *Bernardi 1675* (NY); *Froés 21543* (NY); *Krukoff 811* (NY); *Williams 14480* (US). Wood: *Wurdack & Adderley 42795*, MADw 22429 (= MAD-SJRw 54246) (NY, US).

Pseudanthus divaricatissimus (Muell. Arg.) Benth. Leaf: *Constable 53354* (US); *Ingram s.n.* (NSW). Woody twig: *Constable 53354* (US); *Ingram s.n.* (NSW).

Pseudanthus orientalis F. v. Muell. Leaf: *Clemens 44092* (US); *Wilson 639* (US). Woody twig: *Clemens 44092* (US).

Pseudanthus ovalifolius F. v. Muell. Leaf: *Beauglehole & Orchards 30452* (NSW); *Muir 906* (US). Woody twig: *Beauglehole & Orchards 30452* (NSW); *Muir 906* (US).

Pseudanthus pimelioides Sieb. ex Spreng. Leaf: *Boorman s.n.* (US); *Clemens 42750* (US). Woody twig: *Boorman s.n.* (US); *Clemens 42750* (US); *Constable NSW 55972* (NSW).

Scagea depauperata (Baill.) McPherson. Leaf: *Franc 1642a* (US).

Scagea oligostemon (Guillaum.) Airy Shaw. Leaf: *Guillaumin & Baumann-Bodenheim 11808* (US); *McKee 2352* (US); *McKee 2651* (US).

Stachyandra merana (Airy Shaw) A. Radcliffe-Smith. Leaf: *Baron 6431* (K); *Capuron 23335-5F* (K).

Stachyandra viticifolia (Airy Shaw) A. Radcliffe-Smith. Leaf: *Capuron 20975 SF* (K). Wood: *Capuron 1914.R.4*, CTFw 9069 (TAN).

Stachyandra sp. Wood: *Belin 218.R.6*, CTFw 13786 (TAN).

Stachystemon axillaris George. Leaf: *Blackwell & Griffin 3132* (PERTH).
Stachystemon brachyphyllus Muell. Arg. Leaf: *George 12928* (PERTH).
Stachystemon polyandrus (F. Muell.) Benth. Leaf: *Hnatiuk 761262* (PERTH).
Stachystemon vermiculare Planch. Leaf: *Pritzel s.n.* (US); *Royce 5207* (PERTH).
Tetracoccus dioicus Parry. Leaf: *Moran 13170* (US); *Terrell & Gordon 4004* (US); *Webster & Hildreth 7478* (DAV). Wood: *Campbell 21484* (RSA).
Tetracoccus fasciculatus (Wats.) Croizat var. *fasciculatus*. Leaf: *Johnston 7783* (GH, US); *Webster, 21221* (DAV). Wood: *Johnston 7783*, Aw 23748 (GH, US).
Tetracoccus fasciculatus (Wats.) Croizat var. *hallii* (Brandegee) Dressler. Leaf: *Webster & Hildreth 7460* (DAV); *Wiggins 6617* (US). Wood: *Webster & Hildreth 7460* (DAV).
Tetracoccus ilicifolius Coville & Gilman. Leaf: *Gilman s.n.* (US); *Gilman 2181* (US). Wood: *Gilman 2181* (US).
Voatamalo eugenioides Capuron ex Bosser. Wood: *SF 198 R 259*, (= CTFT 13816, Uw 23104); *SF 5327 R 4* (= CTFT 15079, Uw 23105).
Whyanbeelia terrae-reginae Airy Shaw & Hyland. Leaf: *Irvine 1399* (K). Wood: *Hyland 7945* (K).

APPENDIX 2. Previous anatomical literature on Oldfieldioideae. Comprehensive works abbreviated as follows: G = Gaucher (1902); S = Solereder (1908); MC = Metcalfe & Chalk (1950).

Androstachys Prain. Anonymous (1909); MC; Bolza & Keating (1972); Rao & Raju (1985); Alvin (1987); Alvin & Rao (1987); Dahlgren & van Wyk (1988).
Austrobuxus Miquel (often reported as "*Longetia*," see below). Rothdauscher (1896); G; Dehay (1935); Mathou (1940); Heimsch (1942); MC; Bamber (1974); Rao & Raju (1985).
Celaenodendron Standley. Record (1928); Record (1938); Record & Hess (1943); Hayden (1977).
Croizatia Steyerm. Levin (1986).
Dissiliaria F. Mueller. MC; Dehay (1935); Bamber (1974); Rao & Raju (1985).
Hyaenanche Lambert & Vahl. Pax (1884); G; S; Dehay (1935); Assailly (1954).
Longetia Baillon. Much published anatomical information on "*Longetia*" pertains to *Austrobuxus nitidus* (= *Longetia malayana*); there appears to be no previous anatomical study of *Longetia buxoides* (Baill.) Airy Shaw.
Micrantheum Desfontaines. Pax (1884); G; S; MC; Rao & Raju (1985).
Mischodon Thwaites. G; Gamble (1922); Heimsch (1942); MC; Raju (1984); Rao & Raju (1985).
Neoroepera Mueller Arg. Rothdauscher (1896).
Oldfieldia Bentham. Stone (1904); MC; Assailly (1954); Lebacq & Dechamps (1964); Bolza & Keating (1972); Hayden (1977); Rao & Raju (1985).
Paradrypetes Kuhlm. Milanez (1935); Araujo & Mattos Filho (1984); Levin (1986); Mennega (1987).
Petalostigma F. Mueller. Froembling (1896); Rothdauscher (1896); G; S; Dehay (1935); MC; Bamber (1974); Rao & Raju (1985).
Picrodendron Planchon. Hayden (1977) (q.v. for earlier references); Hakki (1985); Rao & Raju (1985).
Piranhea Baillon. Dehay (1935); Record (1938); MC; Hayden (1977); Pyykkö (1979); Roth (1981); Worbes (1989).
Pseudanthus Sieber ex Sprengel. Pax (1884); G; S; Rao & Raju (1985).
Stachystemon Planchon. Pax (1884); G; MC.
Tetracoccus Engelman ex Parry. Heimsch (1942); MC.

PHYLOGENETIC IMPLICATIONS OF POLLEN ULTRASTRUCTURE IN THE OLDFIELDIOIDEAE (EUPHORBIACEAE)[1]

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ABSTRACT

The pollen structure of members of Euphorbiaceae subfamilies Oldfieldioideae and Phyllanthoideae was studied using scanning and transmission electron microscopy in order to assess taxonomic relationships. We identified 10 palynological characters that appear to have systematic significance. We also identified 37 characters of vegetative morphology and anatomy, mostly based on data obtained by Hayden, and five characters of reproductive morphology, based on data in the literature. Cladistic analysis of the Oldfieldioideae along with selected genera in the Phyllanthoideae, using various putative relatives of the Euphorbiaceae as outgroups, provided great insight into the phylogeny of the Oldfieldioideae. Synapomorphies of this subfamily are all palynological: brevicolporate to pororate or porate apertures, echinate sculpturing, and exine with the interstitium consisting of columellae discontinuous from the foot-layer (where present). With the exception of *Croizatia*, the basal member of the subfamily, all Oldfieldioideae also share the synapomorphies of four or more pollen apertures and no petals; two homoplastic synapomorphies, an exinous foot-layer that is irregular to absent and a caruncle on the seeds, also characterize these genera. A clade consisting of *Paradrypetes* and *Podocalyx* is supported by the synapomorphies of an extremely reduced pollen exine interstitium and sclerified crystalliferous axial xylem parenchyma, whereas the remaining Oldfieldioideae share the synapomorphies of a "microperforate/baculate" tectum consisting of numerous closely appressed rod-shaped elements, some of which are continuous with the columellae and/or echinae; uniformly simple perforation plates; and alternate intervascular pitting. These Oldfieldioideae represent two clades, taxonomically recognized as the tribes Picrodendreae and Caletieae. The Picrodendreae are diagnosed by the synapomorphy of alternate, circular vessel-ray pitting, and except for *Tetracoccus*, the basal member of the clade, also share four additional synapomorphies, all foliar: compound or unifoliolate leaves, well-developed bundle sheath extensions, fimbriate marginal ultimate venation, and well-developed areoles. Within the Picrodendreae, synapomorphies distinguish a South American clade and an African/Madagascan/Indian clade, but do not resolve the position of *Oldfieldia* within the Picrodendreae. The Caletieae share the synapomorphy of stomatal subsidiary cells that have a crenulate (rather than straight) wall nearest the stomatal pore. Within the tribe, the African genus *Hyaenanche* is the basal member, with the remaining genera, all of which are Australasian, being united by the synapomorphy of chambered foliar epidermal cells. The Australasian genera comprise two major clades, but the relationships among these clades and *Petalostigma* are ambiguous. In addition to clarifying relationships within the Oldfieldioideae, these results (1) support the transfer of *Croizatia* and *Paradrypetes* from the Phyllanthoideae to the Oldfieldioideae, (2) support inclusion of *Scagea*, despite its single ovule/locule, in the Oldfieldioideae, (3) demonstrate that *Androstachys* and *Stachyandra* are bona fide members of the Oldfieldioideae rather than belonging in their own family, and (4) indicate that *Neoroepera*, as currently circumscribed, is diphyletic. We propose a revised classification of the subfamily in which all suprageneric taxa are monophyletic according to this phylogeny.

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Light microscopy (LM) of pollen morphology in the Euphorbiaceae (Erdtman, 1952: 165–175; Punt, 1962; Köhler, 1965) has been particularly influential in the development of recent classifications of the family (e.g., Webster, 1975, 1994). More recently, researchers have begun using scanning electron microscopy (SEM) to study pollen of Euphorbiaceae, and though no comprehensive surveys have yet been published, several papers have treated a variety of genera throughout the family, but especially from subfamilies Phyllanthoideae and Oldfieldioideae (Bonnefille & Riollet, 1980; Dechamps et al., 1985; El-Ghazaly & Raj, 1986; Hayden et al., 1984; McPherson & Tirel, 1987; Poole, 1981; Punt, 1980, 1987; Webster, 1984; Webster et al., 1987). However, only two studies of Euphorbiaceae pollen (Hayden et al., 1984; Poole, 1981) have utilized transmission electron microscopy (TEM) to describe the details of exine architecture, and these papers treated only five genera.

We initiated a study of pollen ultrastructure in the Phyllanthoideae and Oldfieldioideae to help resolve intergeneric relationships. These two subfamilies have two ovules in each locule, which is generally regarded as the plesiomorphic condition in contrast to the single ovule per locule found in the remaining three subfamilies. Of the two biovulate subfamilies, Phyllanthoideae is by far the larger and presumably is paraphyletic and basal to the Oldfieldioideae and the uniovulate subfamilies (Webster, 1967, 1975, 1994; Webster et al., 1987).

Details of our pollen study will be published elsewhere (Simpson & Levin, in press). Here we present an overview and phylogenetic analysis of the results, concentrating on the Oldfieldioideae. To evaluate pollen characters and better understand relationships within the subfamily, we also include a phylogenetic analysis of vegetative morphological and anatomical data compiled by Hayden (1980, 1994, this issue) and of selected reproductive characters.

Materials and Methods

TAXA

We examined 40 species in 34 genera with LM and TEM; many of these genera we also examined with SEM (Table 1). Nine genera are members of the Phyllanthoideae sensu Webster (1994), selected to represent the major lineages that have been recognized by prior researchers (e.g., Köhler, 1965; Webster, 1975, 1994; Levin, 1986c). We included *Amanoa guianensis* and *Securinega durissima* because they have echinate pollen reminiscent of pollen of Oldfieldioideae (Webster, 1984; Webster et al., 1987). In addition, we examined *Didymocistus* Kuhlm. because its leaf morphology resembles that of *Hymenocardia* Wallich ex Lindley (Levin, 1986a, b, c) and its wood differs significantly from that of the Aporuseae (Mennega, 1984, 1987), the tribe in which Webster (1975), following Kuhlmann (1940), placed *Didymocistus*. Our selection of Oldfieldioideae includes 25 genera. We chose not to section pollen of *Austrobuxus* and *Picrodendron* because Hayden et al. (1984) published excellent LM, SEM, and TEM photographs of the pollen of these genera. (We note in passing that the pollen Hayden et al. identified as *Austrobuxus carunculatus* (Baillon) Airy Shaw came from specimens McPherson & Tirel (1987) cited as *A. brevipes* Airy Shaw.) Thus we have pollen ultrastructure information on 27 of the 28 genera Webster (1994) included in the Oldfieldioideae. Like Webster (1994), we accept *Paragelonium* as a synonym of *Aristogeitonia* (Radcliffe-Smith, 1987b) and *Stachyandra* as distinct from *Androstachys* (Radcliffe-Smith, 1990). We have been unable to get pollen of *Canaca*, a dubious segregate from *Austrobuxus* (Webster, 1994).

SPECIMEN PREPARATION

Flowers from dried herbarium specimens (cited in Table 1) were rehydrated at room temperature in 1% Aerosol OT for 3–5 days, then fixed and stored in F.A.A. (formalin/acetic acid/ethanol). For LM studies pollen was cleared in Hoyer's mounting medium (Radford et al., 1974) on a microscope slide preparation. LM observations were made using differential interference contrast optics on a Nikon Microphot-FX photomicroscope.

For SEM observations, whole anthers were first dehydrated to 100% ethanol, then gradually infiltrated to 100% methylal (dimethoxymethane) or Freon 113. Anthers were then placed in a metal capsule and critical point-dried (with a Tousimis critical point dryer) using pressurized carbon dioxide as the transition fluid. Pollen grains were tapped onto a stub covered with double-stick tape, sputter-coated with gold/palladium (using a Hummer-4 sputtering apparatus), and photographed on a Hitachi S500 scanning electron microscope. We also examined SEM photographs generously loaned by G. L. Webster.

For TEM observations, whole anthers or isolated pollen were fixed in cold 4% glutaraldehyde in 0.1 M Sorensen's phosphate buffer for 2 hours, fol

TABLE 1. *Palynological characters of investigated Euphorbiaceae. Taxa in Phyllanthoideae are arranged alphabetically. Taxa in Oldfieldioideae are arranged in the order in which they appear in one of our preferred cladograms (Figs. 31–33A). Data are from Simpson & Levin (in prep.) unless otherwise noted; techniques used to observe each taxon are listed following the voucher citation.*

	Pollen				Ektexine			
Taxon	Shape	Size (P × E, μm)	Aperture type	Exine sculpturing	Foot-layer	Interstitium	Tectum	Periapertural thickenings
PHYLLANTHOIDEAE								
Amanoa guianensis Aublet [*Tillett et al. 45256*, DAV] LM, SEM, TEM	Oblate	36 × 42	3-colporate	Echinate, spines 4.1 μm long	Homogeneous, thick (1.0 μm)	Columellate (homologous with echinae?)	Absent (?)	Absent
Amanoa strobilacea Muell. Arg. [*Thomas 4125*, MO] LM, TEM	Oblate	38 × 54	3-colporate	Reticulate	Homogeneous, thick (1.4 μm)	Columellate	Perforate/homogeneous (2.7 μm)	Absent
Antidesma membranaceum Muell. Arg. [*Adam 4973*, MO] LM, TEM	Prolate	23 × 12	3-colporate	Reticulate	Homogeneous, thin (0.11 μm)	Columellate	Perforate/homogeneous (0.30 μm)	Absent
Antidesma venosum Tul. [*Kemp 525*, MO] LM, TEM	Prolate	20 × 12	3-colporate	Reticulate	Homogeneous, thin (0.15 μm)	Columellate	Perforate/homogeneous (0.31 μm)	Absent
Aporusa falcifera Hook. f. [*Soepadmo 41*, MO] LM, SEM, TEM	Globose to sub-prolate	16 × 15	3-colporate	Reticulate	Homogeneous, thin (0.17 μm)	Columellate	Perforate/homogeneous (0.29 μm)	Absent
Didymocistus chrysadenius Kuhlm. [*Dodson & Torres 2961*, MO] LM, SEM, TEM	Globose	12	3-colporate	Rugulate, scabrate, scabrae 0.08 μm long	Homogeneous, thin (0.12 μm)	Columellate	Perforate/homogeneous (0.20 μm)	Absent
Drypetes lateriflora (Sw.) Krug & Urban [*Chambers & Stern 266*, US] LM, SEM	Prolate	30 × 20	3-colporate	Reticulate	Homogeneous, thin (0.18 μm)	Columellate	Perforate/homogeneous (0.37 μm)	Absent
Hyeronima alchorneoides Allemão var. *alchorneoides* [*Croat 51307*, MO] LM, SEM, TEM	Prolate	33 × 19	3-colporate	Reticulate	Homogeneous, thin (0.21 μm)	Columellate	Perforate/homogeneous (0.40 μm)	Absent

TABLE 1. Continued.

Taxon	Pollen: Shape	Pollen: Size (P × E, μm)	Pollen: Aperture type	Pollen: Exine sculpturing	Ektexine: Foot-layer	Ektexine: Interstitium	Ektexine: Tectum	Ektexine: Periapertural thickenings
Hymenocardia acida Tul. [*de Wilde 4044*, MO] LM, SEM, TEM	Oblate	25 × 28	3-porate	Rugulate, scabrate, scabrae 0.07 μm long	Homogeneous, thin (0.18 μm)	Columellate	Perforate/homogeneous (0.26 μm)	Present
Hymenocardia ulmoides Oliver [*Lebrun 2119*, MO] LM, SEM, TEM	Oblate	19 × 21	3-porate	Rugulate, scabrate, scabrae 0.07 μm long	Homogeneous, thin (0.16 μm)	Columellate	Perforate/homogeneous (0.19 μm)	Present
Margaritaria discoidea (Baillon) Webster ssp. *nitida* (Pax) Webster [*Chase 5150*, MO] LM, TEM	Prolate	27 × 22	3-colporate	Reticulate	Homogeneous, thin (0.17 μm)	Columellate	Perforate/homogeneous (0.43 μm)	Absent
Phyllanthus spp.[1,2]	Prolate to globose	13 × 13 to 45 × 33	3-colporate to 60-pantoporate	Reticulate	Details unknown	Columellate	Perforate/homogeneous	?
Securinega durissima J. Gmelin [*Lorence 1397*, MO] LM, SEM, TEM	Oblate	22 × 25	3-colporate	Echinate, spines 1.0 μm long	Homogeneous, thin (0.28 μm)	Columellate	Perforate/homogeneous (0.32 μm)	Absent
OLDFIELDIOIDEAE								
Croizatia naiguatensis Steyerm. [*Berry et al. 4124*, DAV] LM, SEM, TEM	Globose	32	3-brevicolporate	Foveolate, echinate, spines 3.3 μm long	Homogeneous, thick (0.63 μm)	Irregular, discontinuous w/foot-layer	Microperforate/granular (0.24 μm)	Present
Paradrypetes subintegrifolia G. Levin [*Krukoff 4999*, U] LM, SEM, TEM	Oblate	22 × 27	4-brevicolporate, zoni-aperturate	Psilate-wrinkled, echinate, spines 1.4 μm long	Irregular (0.12 μm)	Absent	Imperforate (0.35 μm)	Absent
Podocalyx loranthoides Klotzsch [*Vicira et al. 195*, MO] LM, SEM, TEM	Oblate	22 × 25	4-porate, zoniaperturate	Psilate-wrinkled, echinate, spines 2.8 μm long	Irregular (0.11 μm)	Absent	Microperforate/baculate (0.33 μm)	Absent
Tetracoccus dioicus C. Parry [*Henry & Dice s.n.* (8 April 1980), SD] LM, SEM, TEM	Globose	46 × 47	4-pororate, zoniaperturate	Verrucate, echinate, spines 4.7 μm long	Irregular (0.35 μm)	Irregular, discontinuous w/foot-layer	Microperforate/baculate (0.63 μm)	?

TABLE 1. *Continued.*

Taxon	Pollen				Ektexine			
	Shape	Size (P × E, μm)	Aperture type	Exine sculpturing	Foot-layer	Interstitium	Tectum	Periapertural thickenings
Parodiodendron marginivillosum (Speg.) Hunz. [*Ververst & Cuezzo 7610*, US] LM, SEM, TEM	Oblate	24 × 27	ca. 7-porate, zoni-aperturate	Verrucate, echinate, spines 3.1 μm long	Absent	Irregular, discontinuous w/foot-layer	Microperforate/baculate (1.1 μm)	Absent
Picrodendron baccatum (L.) Krug & Urban[4] LM, SEM, TEM	Oblate	26 × 29	5–8-brevicolporate, zoni-aperturate	Verrucate, echinate, spines 3 μm long	Irregular, thin	Irregular, discontinuous w/foot-layer	Microperforate/baculate (0.6–0.8 μm)	Absent
Piranhea trifoliata Baillon [*Berg et al. P19789*, MO] LM, SEM, TEM	Oblate	32 × 35	6-porate, zoniaperturate	Verrucate, echinate, spines 2.7 μm long	Absent	Irregular	Microperforate/baculate (0.39 μm)	?
Celaenodendron mexicanum Standley [*Perez & Chang 1776*, MO] LM, TEM	Sub-oblate	39 × 40	7(8)-porate, zoni-aperturate	Echinate, spines 2.9 μm long	Absent	Irregular	Microperforate/baculate (0.59 μm)	Absent
Oldfieldia africana Benth. & Hook. f. [*Fox 157*, K] LM, SEM, TEM	Oblate	28 × 30	5–6-porate, zoni-aperturate	Verrucate, echinate, spines 3.5 μm long	Absent	Irregular	Microperforate/baculate (0.44 μm)	Absent
Androstachys johnsonii Prain [*Balsinhas 3549*, K] LM, SEM, TEM	Globose	50	5–7-pantoporate	Psilate, echinate, spines 1.1 μm long	Homogeneous, thin (0.07 μm)	Columellate	Microperforate/homogeneous (0.36 μm)	Absent
Stachyandra merana (Airy Shaw) R.-Sm. [*Capuron 23335-SF*, P] LM, SEM, TEM	Globose	44	4–6-porate, zoni-aperturate	Echinate, spines 1.4 μm long	Absent	± Irregular	Microperforate/homogeneous (0.52 μm)	Absent
Stachyandra rufibarbis (Airy Shaw) R.-Sm. [*Capuron 9177-SF*, P] LM, TEM	Globose	46	5–7-porate, zoni-aperturate	Echinate, spines 0.9 μm long	Absent	Irregular	Microperforate/homogeneous (0.50 μm)	Absent
Voatamalo eugenioides Bosser [*Capuron 22327-SF*, K] LM, TEM	Globose	44	5–6-porate, zoni-aperturate	Echinate, spines 3.3 μm long	Irregular to absent (0.14 μm)	Irregular, discontinuous w/foot-layer	Microperforate/baculate (0.38 μm)	?

TABLE 1. Continued.

Taxon	Pollen: Shape	Pollen: Size (P × E, μm)	Pollen: Aperture type	Pollen: Exine sculpturing	Ektexine: Foot-layer	Ektexine: Interstitium	Ektexine: Tectum	Ektexine: Periapertural thickenings
Mischodon zeylanicus Thwaites [*Waas 336*, MO] LM, SEM, TEM	Globose	38	5 7-porate, zoni-aperturate	Echinate, spines 3.8 μm long	Irregular (0.25 μm)	Irregular, discontinuous w/foot-layer	Microperforate/baculate (0.44 μm)	?
Aristogeitonia monophylla Airy Shaw [*Faden et al. 45256*, K] LM, TEM	Oblate	30 × 34	5–7-brevicolporate, zoni-aperturate	Echinate, spines 4.1 μm long	Absent	Irregular	Microperforate/baculate (0.24 μm)	Absent
Hyaenanche globosa (Gaertner) Lambert [*Lavranos & Bleck 20843A*, MO] LM, SEM, TEM	Suboblate	40 × 42	6–7-brevicolporate, zoni-aperturate	Verrucate, echinate, spines 2.1 μm long	Irregular (0.34 μm)	Irregular, discontinuous w/foot-layer	Microperforate/baculate (0.47 μm)	Absent
Austrobuxus spp.[1,2,3,4] LM, SEM, TEM	Oblate	25 × 28 to 29 × 33	5–7-porate, zoni-aperturate	Foveolate, echinate, spines 3–5.5 μm long	Irregular	Irregular, discontinuous w/foot-layer	Microperforate/baculate (0.9–1.4 μm)	?
Whyanbeelia terrae-reginae Airy Shaw & Hyland [*Hyland 3041*, DAV] LM, SEM, TEM	Oblate	27 × 30	5–6-porate, zoni-aperturate	Verrucate, echinate, spines 4.1 μm long	Absent	Irregular	Microperforate/baculate (0.48 μm)	Present
Longetia buxoides Baillon [*McPherson 3789*, MO] LM, SEM, TEM	Oblate	27 × 30	6–7-colporate, zoni-aperturate	Psilate-wrinkled, scabrate, scabrae 0.4 μm long	Absent	Irregular	± Imperforate (0.84 μm)	Present
Choriceras majus Airy Shaw [*Hyland 10633*, K] LM, SEM, TEM	Oblate	26 × 28	6-porate, zoniaperturate	Psilate-wrinkled, scabrate, scabrae 0.2 μm long	Absent	Irregular	Microperforate/homogeneous (0.43 μm)	Present
Dissiliaria baloghioides F. Muell. [*MacPherson s.n.* (23 Jan 1980), QRS] LM, TEM	Subglobose	36 × 38	5–6-porate, zoni-aperturate	Echinate, spines 4.1 μm long	Absent	Irregular	Microperforate/baculate (0.75 μm)	Present
Petalostigma pubescens Domin [*Speck 1818*, K] LM, SEM, TEM	Oblate	32 × 34	5-porate, zoniaperturate	Echinate, spines 0.9 μm long	Absent	Irregular	Microperforate/baculate (0.38 μm)	Absent

TABLE 1. Continued.

Taxon	Pollen				Ektexine			
	Shape	Size (P × E, μm)	Aperture type	Exine sculpturing	Foot-layer	Interstitium	Tectum	Periapertural thickenings
Petalostigma quadriloculare F. Muell. [*Mocanochie 1993*, K] LM, TEM	Oblate	32 × 34	5–6-porate, zoni-aperturate	Echinate, spines 1.0 μm long	Absent	Irregular	Microperforate/baculate (0.51 μm)	Absent
Neoroepera buxifolia Muell. Arg. [*White 12095*, US] LM, SEM, TEM	Globose	33	16–20-pantoporate	Foveolate, echinate, spines 5.1 μm long	Absent	Irregular	Microperforate/baculate (0.63 μm)	?
Kairothamnus phyllanthoides (Airy Shaw) Airy Shaw [*Streimann NFG 24462*, K] LM, SEM, TEM	Globose	26	10–12-pantoporate	Foveolate, echinate, spines 1.8 μm long	Homogeneous, thick (0.61 μm)	Irregular, discontinuous w/foot-layer	Microperforate/granular (0.21 μm)	Absent
Scagea oligostemon (Guillaumin) McPherson [*Webster 19181*, DAV] LM, SEM, TEM	Globose	30	16–20-pantoporate	Foveolate, echinate, spines 1.9 μm long	Homogeneous, thick (0.70 μm)	Irregular, discontinuous w/foot-layer	Microperforate/granular (0.19 μm)	Absent
Neoroepera banksii Benth. [*Hyland 6945*, K] LM, TEM	Globose	36	ca. 25-pantoporate	Echinate, spines 3.7 μm long	Homogeneous, thick (0.98 μm)	Irregular, discontinuous w/foot-layer	Microperforate/granular (0.26 μm)	Absent
Micrantheum hexandrum Hook. f. [*Briggs & Johnson 4419*, DAV] LM, SEM, TEM	Globose	34	30 40-pantoporate	Foveolate, echinate, spines 3.0 μm long	Homogeneous, thick (1.5 μm)	Irregular, discontinuous w/foot-layer	Microperforate/granular (0.33 μm)	Absent
Pseudanthus divaricatissimus (Muell. Arg.) Benth. [*Coveny 5253*, DAV] LM, SEM, TEM	Globose	23	10–14-pantoporate	Foveolate, echinate, spines 1.2 μm long	Homogeneous, thick (0.65 μm)	Irregular, discontinuous w/foot-layer	Microperforate/granular (0.22 μm)	Absent
Stachystemon polyandrus (F. Muell.) Benth. [*Young Y-325*, DAV] LM, TEM	Globose	22	12-pantoporate	Echinate, spines 1.8 μm long	Homogeneous, thin (0.34 μm)	Irregular, discontinuous w/foot-layer	Microperforate/granular (0.14 μm)	Absent

[1] Punt, 1962, 1980, 1987; [2] Köhler, 1965; [3] Martin, 1974; [4] Hayden et al., 1984.

lowed by several rinses in buffer and further fixation in 2% osmium tetroxide for 2 hours. The material was then quickly rinsed twice in buffer, progressively dehydrated to 100% ethanol, and infiltrated (via a gradation series) with Spurr's resin (Spurr, 1969). The material was polymerized in BEEM capsules at 65°C for 12–18 hours. Sections 0.5 μm thick were stained with 1% toluidine blue and mounted on a slide for light microscope observations. Anthers were then ultrathin-sectioned (ca. 95 nm thick) using a Diatome diamond knife on a Reichert Ultracut-E ultramicrotome, mounted on uncoated hexagonal 200 mesh copper grids, and post-stained with uranyl acetate (saturated solution in 50% ethanol, 15 minutes) and lead citrate (0.2% aq., 7 minutes). To inhibit stain precipitation, grids were gently and quickly washed in a running stream of filtered, distilled water between and after post-staining changes. Observations and photographs were made on a Phillips EM 410 transmission electron microscope.

PHYLOGENETIC ANALYSIS

We analyzed our data using Wagner parsimony as implemented by PAUP version 3.1 (Swofford, 1993) and HENNIG86 version 1.5 (Farris, 1988). With PAUP we performed heuristic searches (options *Mulpars*, *Maxtree* = 250, and *Hold* = 5) starting with both closest and random (10 replicates) addition sequences followed by tree bisection-reconnection (TBR) branch-swapping. With HENNIG86 we used the options *whennig** and *bb* to implement similar branch swapping. In addition, we iteratively used the options *xsteps w* and *ccodes* followed by *whennig* and *bb* to explore the effect of Farris's (1969) sequential weighting of characters, in which the weight of each character is adjusted according to its homoplasy on the previously generated trees. We analyzed character changes on alternative trees using MacClade version 3.0 (Maddison & Maddison, 1992).

Results and Discussion

CHARACTER DEFINITION

The characters and character states used in our cladistic analysis are listed in Table 2. Of the 52 characters, 45 are binary characters. We treated all but one of the seven multistate characters as unordered. The exception is character 24, leaf blade; see below for an explanation of how we coded this character. The following is a discussion of the rationale for our decisions of character/character state definition for the palynological, selected vegetative morphological and anatomical, and reproductive morphological characters.

Palynological characters. Table 1 summarizes the pollen morphology of the genera we examined, supplemented by other published accounts. More detailed information can be found in Simpson & Levin (in prep.). We recognized 10 palynological characters.

1. Pollen shape. This character distinguishes taxa such as *Hyeronima* (Figs. 1, 2) that have strongly prolate grains (polar axes longer than equatorial axes) from those such as *Neoroepera* (Figs. 3, 4), *Parodiodendron* (Figs. 5, 6), *Androstachys* (Figs. 7, 8), *Micrantheum* (Figs. 9, 10), and *Pseudanthus* (Figs. 11, 12), that have grains ranging from globose to oblate (equatorial axes longer than polar axes). We combined the latter two shape types in a single character state because of the lack of a clear discontinuity between globose, suboblate, and oblate shapes (see Table 1).
2. Pollen aperture number. The number of pollen apertures is either three (e.g., *Hyeronima*, Figs. 1, 2) or more than three (e.g., *Neoroepera*, Figs. 3, 4; *Androstachys*, Figs. 7, 8). We selected the presence of three apertures as a character state because of its widespread occurrence among the dicotyledons (Walker & Doyle, 1975). For those taxa with more than three apertures, the number ranges from four (e.g., *Paradrypetes*; Levin, 1992: fig. 1) to 20 or more (e.g., *Neoroepera*, Figs. 3, 4; *Micrantheum*, Figs. 9, 10; see also Table 1). Because we could see no clear discontinuity in aperture numbers among these latter taxa, we treated the presence of 4–20 or more apertures as a single character state.
3. Aperture position. This character distinguishes between zoni-aperturate grains (apertures present only along the equatorial plane; e.g., *Hyeronima*, Fig. 1) and pan-aperturate grains (apertures positioned throughout surface; e.g., *Neoroepera*, Figs. 3, 4; *Pseudanthus*, Figs. 11, 12).

Reports on aperture number and distribution of *Androstachys* differ considerably. Erdtman (1952: 167) described the pollen as polyforate, i.e., pantoporate with more than 12 apertures (not oligoforate, i.e., with 12 or fewer pores, as misquoted by Dahlgren & van Wyk, 1988), with the pores faintly defined and covered with granulate membranes. Köhler (1965), studying the same sample, described the pollen as more-or-less pantoporate

TABLE 2. Characters and character states used in cladistic analysis of the Euphorbiaceae.

1. Pollen shape: 0 = oblate-globose; 1 = prolate.
2. Aperture number: 0 = 3; 1 = >3.
3. Aperture position: 0 = zoni-aperturate; 1 = pan-aperturate.
4. Aperture shape: 0 = colporate; 1 = brevicolporate-porate.
5. Sculpturing (spinal): 0 = absent; 1 = minute (<0.5 μm); 2 = large (>0.9 μm).
6. Sculpturing (nonspinal): 0 = reticulate; 1 = foveolate; 2 = rugulate; 3 = verrucate; 4 = psilate-wrinkled.
7. Foot-layer: 0 = homogeneous/thin; 1 = homogeneous/thick; 2 = irregular-absent.
8. Interstitium: 0 = continuous with foot-layer; 1 = discontinuous with foot-layer; 2 = absent.
9. Tectum: 0 = perforate/homogeneous; 1 = microperforate/homogeneous; 2 = microperforate/baculate; 3 = microperforate/granular; 4 = imperforate; 5 = absent.
10. Ektexinous periapertural thickenings: 0 = absent; 1 = present.
11. Porosity: 0 = diffuse; 1 = ring.
12. Perforation plates: 0 = mixed scalariform and simple; 1 = all simple.
13. Intervascular pits: 0 = transitional; 1 = alternate.
14. Intervascular pits: 0 = small, 1 = larger.
15. Fibers: 0 = nonseptate; 1 = septate.
16. Rays: 0 = heterocellular; 1 = homocellular erect.
17. Rays: 0 = not aggregate; 1 = aggregate.
18. Vessel-ray pits: 0 = irregular shape and pattern; 1 = circular and alternate.
19. Crystalliferous ray cells: 0 = unsclerified; 1 = sclerified.
20. Axial parenchyma: 0 = present; 1 = absent.
21. Crystalliferous axial xylem parenchyma: 0 = sclerified; 1 = unsclerified.
22. Secondary phloem sclerenchyma: 0 = present; 1 = absent.
23. Cotyledons: 0 = wider than radicle; 1 = narrower than radicle.
24. Leaf blade: 0 = simple; 1 = compound; 2 = unifoliolate.
25. Phyllotaxy: 0 = alternate; 1 = opposite.
26. Epidermal mucilage: 0 = present; 1 = absent.
27. Epidermal cells: 0 = undivided; 1 = chambered.
28. Epidermal anticlinal walls: 0 = straight; 1 = undulate.
29. Stomatal pattern: 0 = paracytic or brachyparacytic; 1 = anomocytic; 2 = anisocytic.
30. Subsidiary cell anticlinal wall (nearest stomatal pore): 0 = straight; 1 = crenulate.
31. Phloem fibers of primary vein: 0 = lignified; 1 = thick-walled and unlignified; 2 = thin-walled and unlignified.
32. Crystals in mesophyll: 0 = present; 1 = absent.
33. Bundle sheath extension: 0 = absent; 1 = present.
34. Bundle sheath extension crystals: 0 = absent; 1 = prismatic.

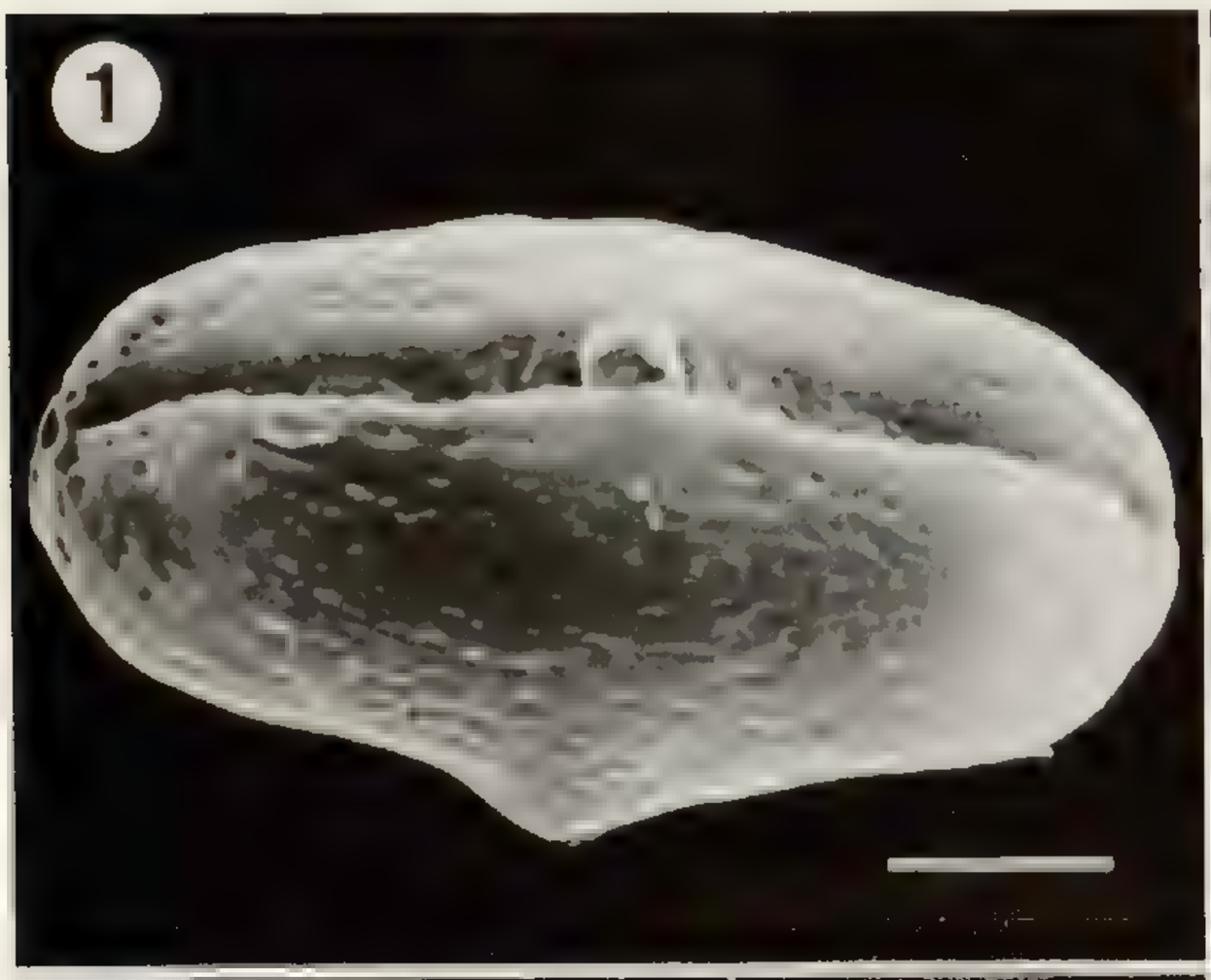
TABLE 2. Continued.

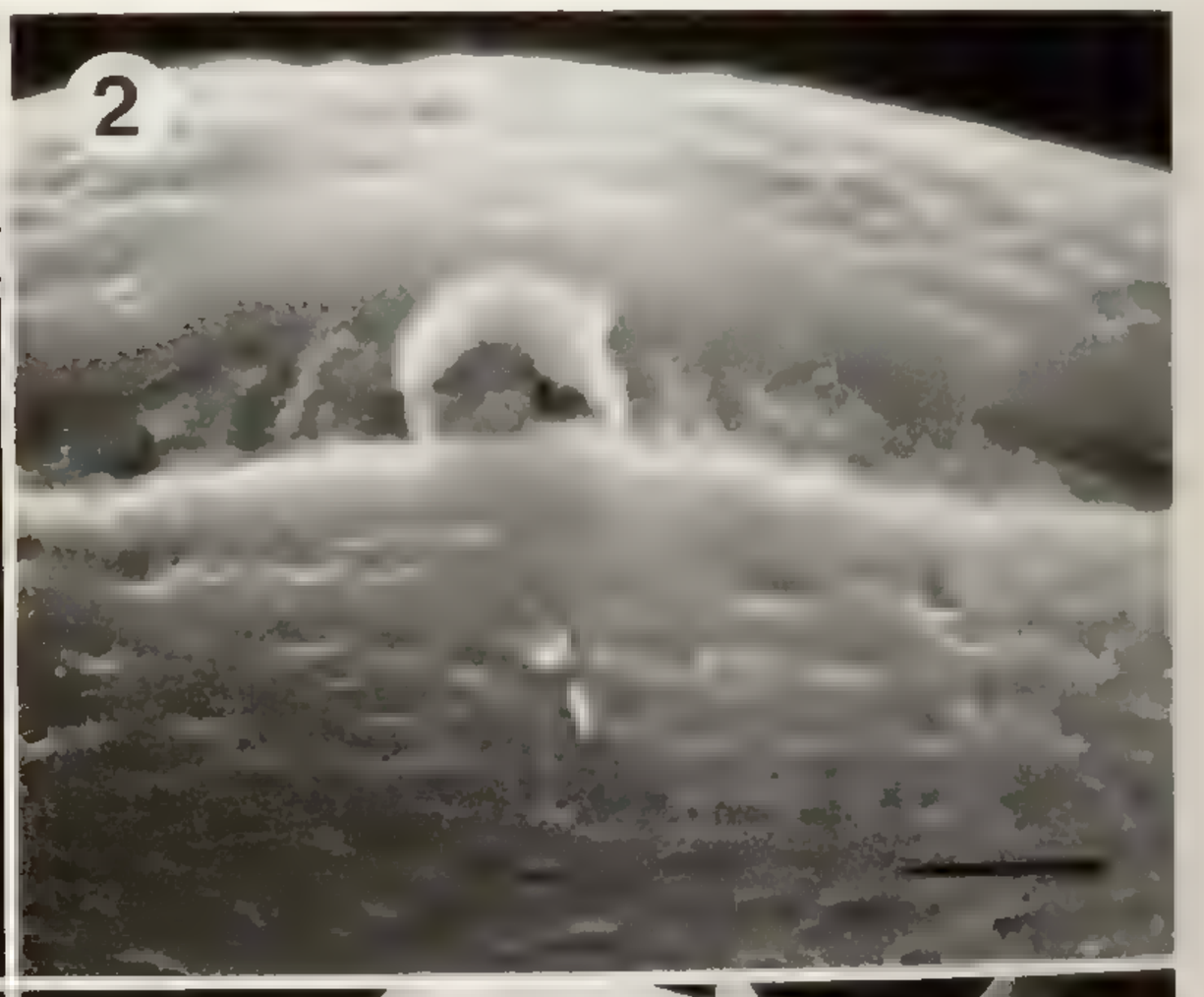
35. Venation: 0 = brochidodromous; 1 = irregularly brochidodromous.
36. Venation: 0 = irregularly brochidodromous; 1 = kladodromous.
37. Venation: 0 = all others; 1 = reticulodromous or hyphodromous.
38. Intramarginal vein: 0 = absent; 1 = present.
39. Marginal ultimate venation: 0 = looped or incomplete; 1 = fimbriate.
40. Tertiary venation: 0 = irregular; 1 = orthogonal.
41. Vein order beyond tertiaries: 0 = distinguishable; 1 = indistinguishable in reticulum.
42. Areoles: 0 = imperfect or incomplete; 1 = well developed.
43. Tracheoid idioblasts: 0 = absent; 1 = present.
44. Columnar foliar sclereids: 0 = absent; 1 = present.
45. Stipules: 0 = present; 1 = absent.
46. Stipules: 0 = on stem; 1 = epipetiolar.
47. Raphides: 0 = absent; 1 = present.
48. Sexuality: 0 = dioecious; 1 = monoecious.
49. Petals: 0 = present; 1 = absent.
50. Ovules/locule: 0 = two; 1 = one.
51. Caruncle on seeds: 0 = absent; 1 = present.
52. Endosperm: 0 = abundant; 1 = scanty or absent.

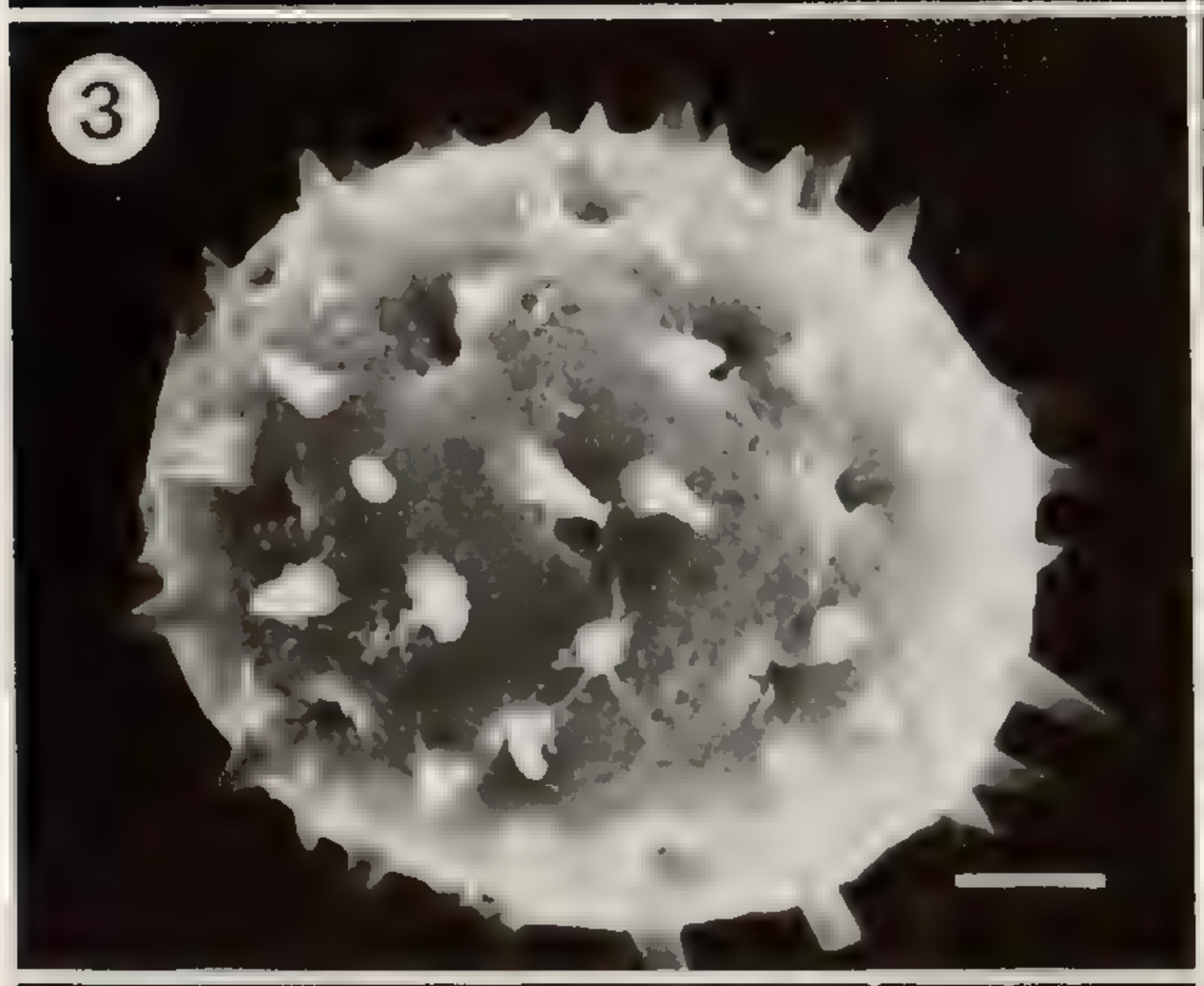
or possibly dizonoporate, with 14–18 inconspicuous, variably shaped apertures covered with granular or smooth membranes. Punt (1962), who studied different material, considered the pollen inaperturate. All these authors used only LM. Dahlgren & van Wyk (1988) used both LM and SEM to investigate yet another sample and found that most grains were inaperturate but some had a few places where the thin tectum apparently was torn to form a small "pore" with a granular membrane.

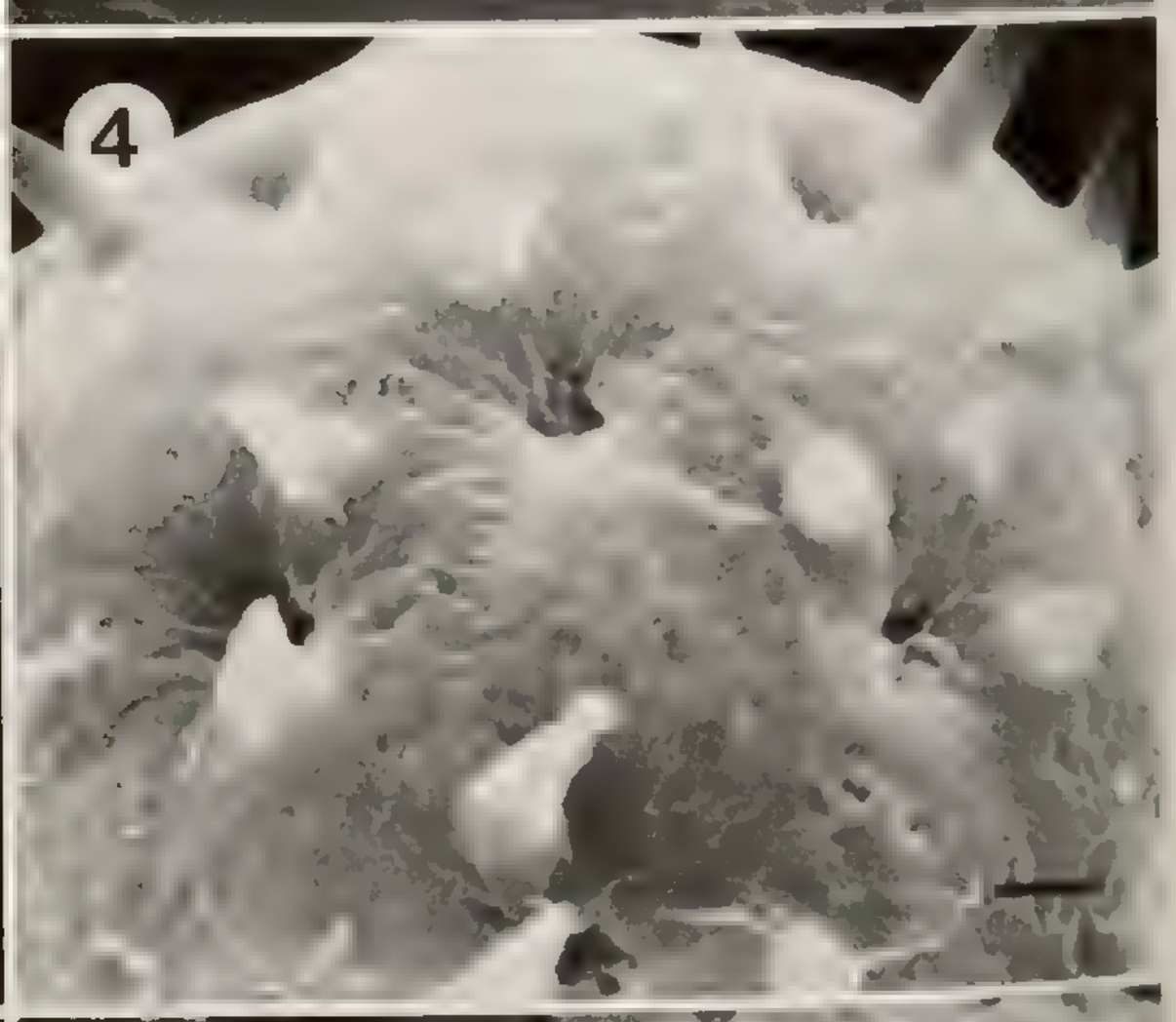
We examined pollen of both *Androstachys* and *Stachyandra* (= *Androstachys* subg. *Archandrostachys* Leroy), which is clearly closely related to *Androstachys* but has more primitive leaf morphology and flowers (Leroy, 1976; Dahlgren & van Wyk, 1988; Radcliffe-Smith, 1990). Our SEM observations indicate that all pollen in our sample of *Androstachys johnsonii* is pantoporate, usually with 5–7 apertures (Figs. 7, 8). With LM these apertures were often extremely inconspicuous, but could be resolved using Herr's clearing fluid (Herr, 1971). *Stachyandra*, in contrast, has pores easily seen with LM. Both species we examined were zoni-aperturate, *S. merana* with 4–6 pores and *S. rufibarbis* with 5–7 pores.

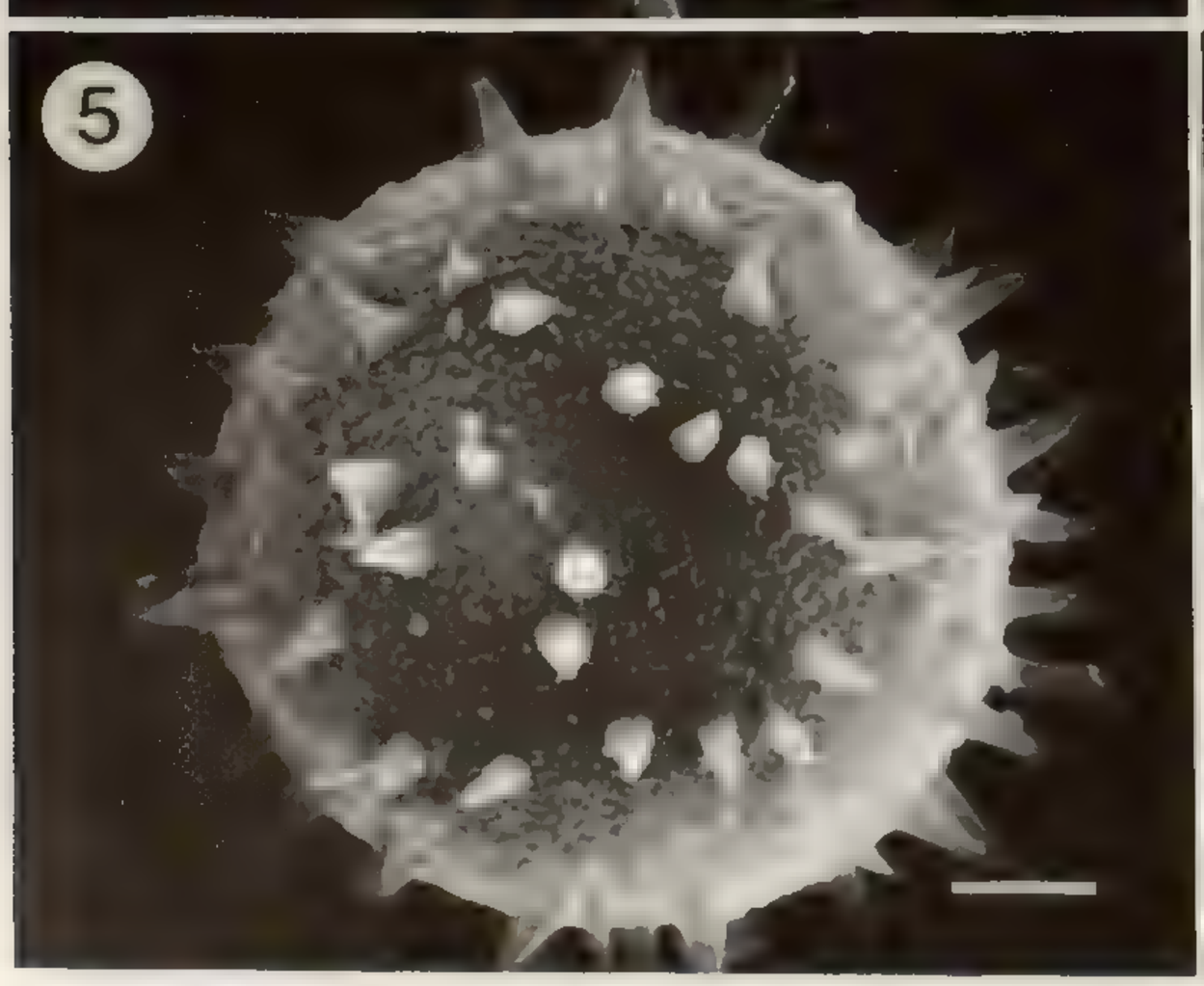
Erdtman (1952: 170), studying what he

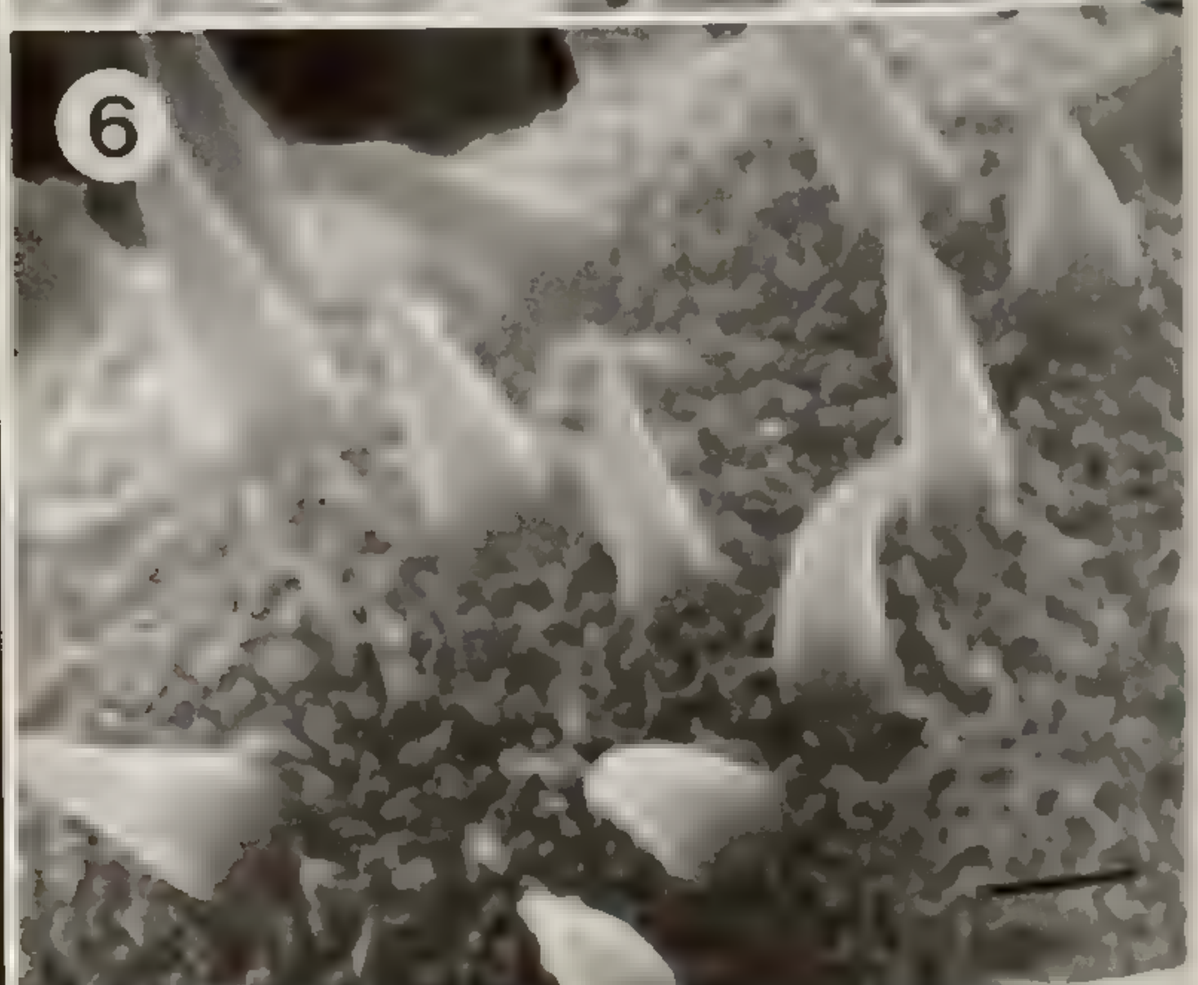






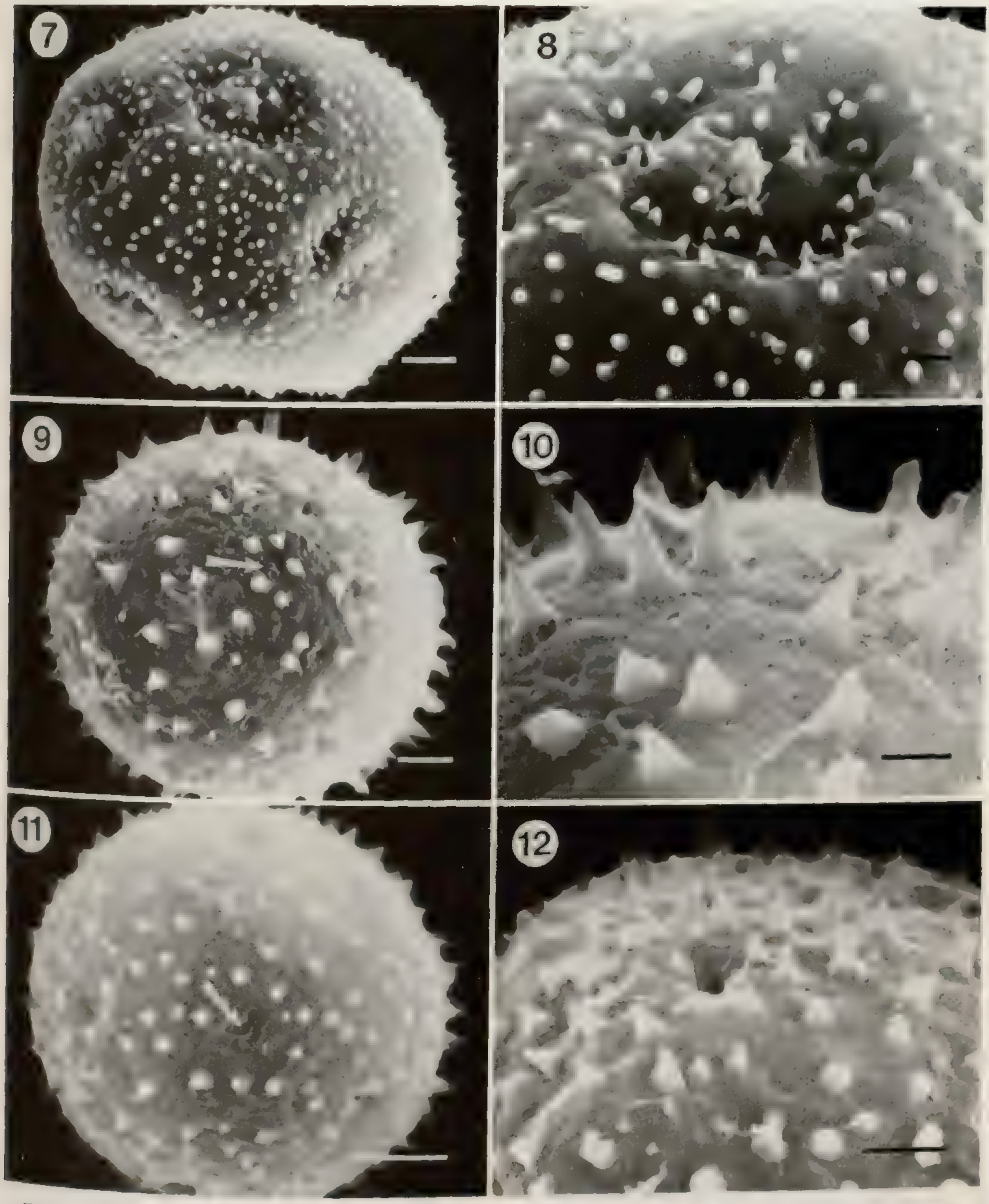






FIGURES 1–6. Scanning electron micrographs of pollen of Euphorbiaceae subfamily Phyllanthoideae (1, 2) and subfamily Oldfieldioideae (3–6).—1, 2. *Hyeronima alchorneoides*.—3, 4. *Neoroepera buxifolia*.—5, 6. *Parodiodendron marginivillosum*. Scale bars in 1, 3, 5 = 5 μm; in 2, 4, 6 = 2 μm.

called *Petalostigma pubescens*, and Punt (1962) and Köhler (1965), studying what they called *P. quadriloculare*, reported that the apertures of *Petalostigma* do not lie exactly in the equatorial plane. Our observations are not entirely consistent with theirs. In *P. pubescens* we found that some of the apertures indeed lay outside the equatorial plane, but in *P. quadriloculare* all the apertures were strictly equatorial. Prior to Airy Shaw's revision of the genus in 1976, many collections were misidentified (Airy Shaw, 1976). All of



FIGURES 7–12. Scanning electron micrographs of pollen of Euphorbiaceae subfamily Oldfieldioideae.—7, 8. *Androstachys johnsonii*. 9, 10. *Micrantheum hexandrum*.—11, 12. *Pseudanthus divaricatissimus*. Arrow in Figure 11 indicates an aperture. Scale bars in 7, 9, 11 = 5 μm; in 8, 10, 12 = 2 μm.

our samples came from specimens at Kew annotated by Airy Shaw. Unfortunately, he did not cite any of the material studied by the other palynologists, so we cannot determine if differences in observations reflect variation within species or simply misidentifications. We have therefore tentatively coded the pollen of *Petalostigma* as zoni-aperturate. It is possible, however, that the aperture distribution in *Petalostigma* may represent a transition between zoni-aperturate and pan-aperturate, particularly if the species themselves are polymorphic.

Among the species we sampled, except for *Androstachys*, taxa with 4–7 apertures are zoni-aperturate or essentially so, whereas those

with 10 or more apertures are all pan-aperturate (see Table 1). A literature review, summarized in Simpson & Levin (in prep.), shows this pattern to be generally true, the sole exception we are aware of being some species of *Pseudanthus*, which are pan-aperturate with 6–8 apertures.

4. Aperture shape. Apertures were either elongate and colporate (e.g., *Hyeronima*, Figs. 1, 2) or considerably shorter, intergrading from brevicolporate to pororate to porate (e.g., *Neoroepera*, Figs. 3, 4; *Pseudanthus*, Figs. 11, 12).

We divided exine wall sculpturing into the following two characters:

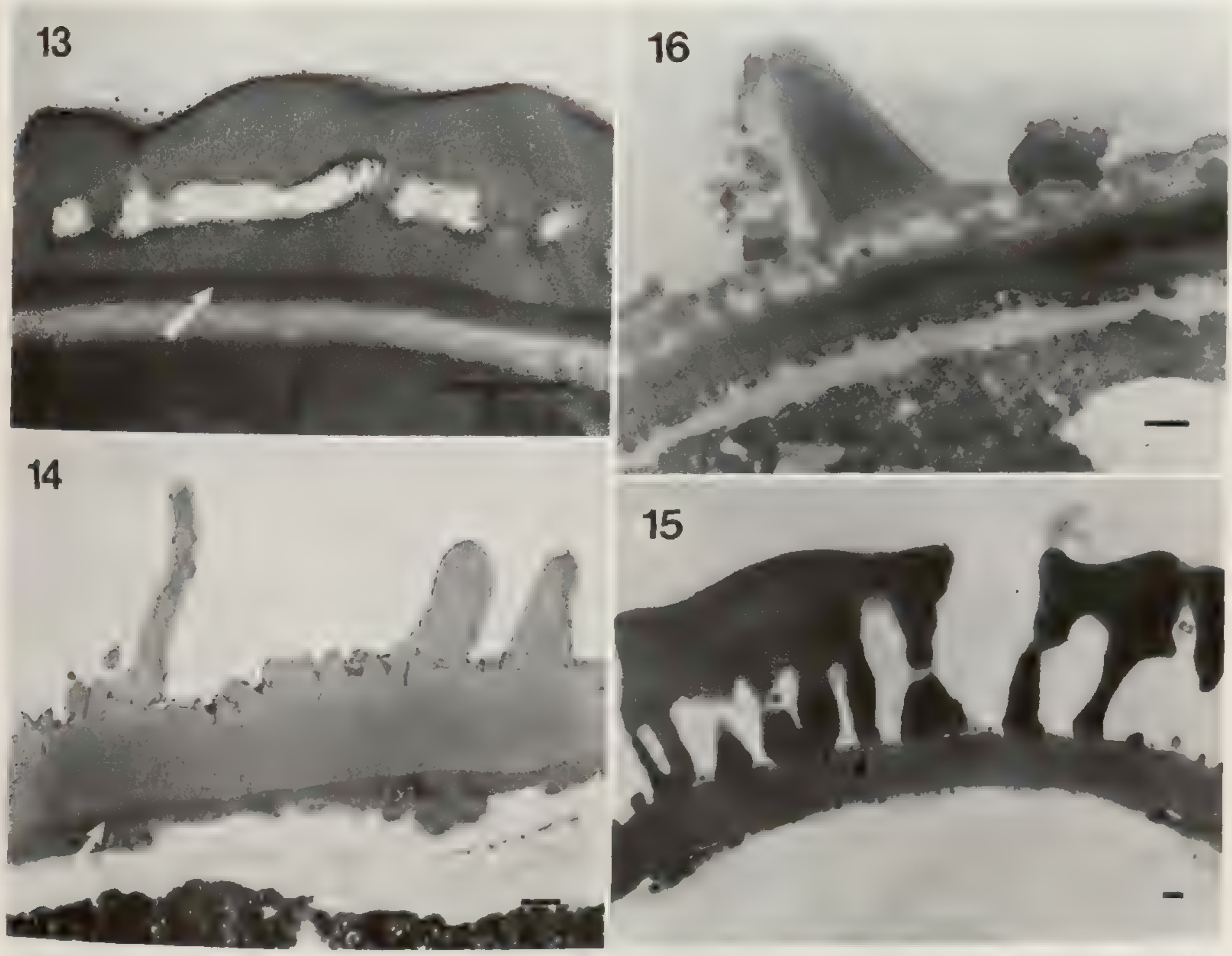
5. Sculpturing (spinal). Radially elongate, mostly sharply tapering spines are absent from some investigated Euphorbiaceae (e.g., *Hyeronima*, Figs. 1, 2). However, a number of taxa possess spines, the length of which ranges from relatively long (e.g., *Parodiodendron*, Figs. 5, 6) to short (e.g., *Androstachys*, Figs. 7, 8). Because we found a clear discontinuity between short tectal spines (< 0.5 μm long, called "scabrae" by Reitsma, 1970) and spines of greater length (> 0.9 μm, called "echinae" by Reitsma), we coded these as separate states (see Table 1).
6. Sculpturing (nonspinal). This character denotes the sculpturing of the outer exine surface between spines (if present) or the general surface sculpturing if spines are not present. Reticulate pollen has a perforate tectum in which a network of muri could be delimited, regardless of the relative size of the perforations (e.g., *Hyeronima*, Figs. 1, 2). Foveolate pollen also has a perforate tectum but with no clear indication of tectal muri (see *Croizatia*, Webster et al., 1987: figs. 2, 3). In recognizing both states we differentiated between micropores, tiny perforations in the tectum present in most pollen, and the considerably larger perforations found in reticulate and foveolate pollen. Rugulate pollen has a tectum that appears conspicuously wrinkled or folded; a regular pattern of perforations is lacking (see *Hymenocardia* and *Didymocistus*, figs. 1–6 in Levin & Simpson, 1994, this issue). The remaining states lack large perforations, though they may be microperforate. Verrucate pollen has the tectal surface covered with small rounded processes, or verrucae (see *Tetracoccus*, Webster et al., 1987: fig. 5). Some taxa were coded "?" because we were unable to determine from the micrographs whether the pollen was verrucate or foveolate. The sculpturing of *Picrodendron* might be termed "vermiform" in that the tectal processes are somewhat elongated and twisted, but we coded it as verrucate because of its basic similarity to that pattern and because the sculpturing of *Parodiodendron* (Fig. 6) is somewhat transitional. Psilate-wrinkled pollen has a relatively smooth tectum apparently devoid of (nonspinal) sculpturing (e.g., *Androstachys*, Fig. 8), or may appear somewhat wrinkled, perhaps a function of specimen preparation.

We treated the structure of the exine wall as four separate characters (7–10). The first three correspond to the three general regions of the ektexine between the apertures.

7. Foot-layer. Several taxa have a typical continuous, homogeneous ektexinous foot-layer (e.g., *Antidesma*, Fig. 13; *Amanoa*, Figs. 14, 15; *Croizatia*, Fig. 16). Analysis of the variation in foot-layer thickness within and among these taxa (Fig. 17) shows four distinct size classes that could be validly recognized as character states (Stevens, 1991). In preliminary cladistic analyses we tried dividing this character into four states, lumping the two largest size classes into a single state, or combining all but the smallest size class into a single state. Because the resulting trees were the same in all three cases and so few taxa fell into the two largest size classes, we decided to recognize only two states (< 0.5 μm and > 0.5 μm) for the homogeneous foot-layer.

In the remaining taxa, the ektexinous foot-layer was very irregular, consisting of discontinuous, almost granular elements (Figs. 18–23). At one extreme (e.g., *Tetracoccus*, Fig. 19), this irregular foot-layer was present around the entire grain; at the other extreme (e.g., *Oldfieldia*, Fig. 18), the ektexinous foot-layer was essentially absent, represented only by rare and scattered granules. Various intermediates were present (e.g., *Longetia*, Fig. 23), preventing us from distinguishing the two extremes as separate states. The innermost layer of ektexine in both *Podocalyx* (Fig. 20) and *Paradrypetes* (Fig. 21) we interpreted as an irregular foot-layer (see character #8, below).

Endexine was found as a thin to moderately thick basal layer (usually thickening at the



FIGURES 13–16. Transmission electron micrographs of pollen of Euphorbiaceae subfamily Phyllanthoideae (13–15) and subfamily Oldfieldioideae (16).—13. *Antidesma membranaceum*.—14. *Amanoa guianensis*.—15. *Amanoa strobilacea*.—16. *Croizatia naiguatensis*. Arrow in Figure 13 indicates endexine. Scale bars = 0.5 μm.

aperture periphery) in almost all taxa (see *Antidesma*, Fig. 13; *Oldfieldia*, Fig. 19) and does not seem to be of taxonomic significance.

8. Interstitium. The interstitium may consist of columellae that are continuous with the foot-layer, as in the typical "tectate-columellate" architecture (e.g., *Antidesma*, Fig. 13; *Amanoa strobilacea*, Fig. 15), or an evident discontinuity may occur between the columellar elements and foot-layer (e.g., *Tetracoccus*, Fig. 19; *Scagea*, Fig. 24; *Stachystemon*, Fig. 25). In no case did the columellae appear to be discontinuous with the tectal region. Thus, in taxa such as *Podocalyx* (Fig. 20) and *Paradrypetes* (Fig. 21), in which the exine consists of a relatively thick outer layer discontinuous from a thin, granular inner layer, we interpreted the inner layer as an irregular foot-layer and the interstitium as absent.
9. Tectum. Two variables affect tectum structure: its degree of perforation and its organization. The tectum of some taxa (e.g., *Antidesma*, Fig. 13; *Amanoa strobilacea*, Fig. 15) is homogeneous and penetrated by large perforations rather than microperforations, a state we called "perforate/homogeneous." (Because of the large size of the perforations, they may be absent in some TEM sections making the tectum appear imperforate.) Among taxa with a microperforate tectum, three states were apparent. The tectum may be "microperforate/homogeneous" (e.g., *Androstachys*, Fig. 22); "microperforate/baculate," consisting of numerous closely appressed rod-shaped elements, some of which are continuous with the columellae and/or echinae (e.g., *Oldfieldia*, Fig. 18; *Tetracoccus*, Fig. 19); or "microperforate/granular," consisting of small, irregular, globular to tabular elements (e.g., *Croizatia*, Fig. 16; *Scagea*, Fig. 24; *Stachystemon*, Fig. 25). Still other taxa have a tectum that is "imperforate," lacking both perforations and microperforations (e.g., *Paradrypetes*, Fig. 21;

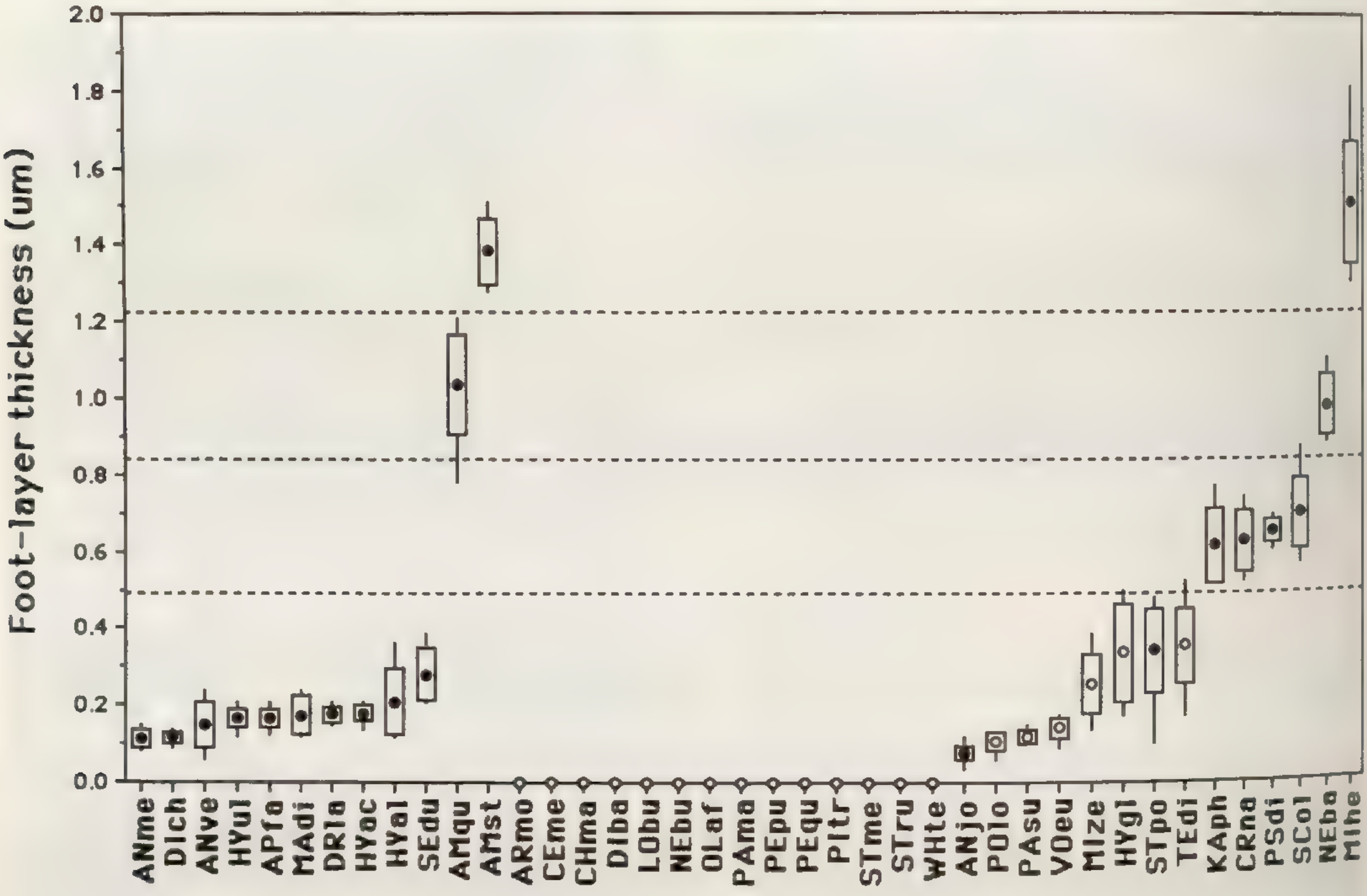
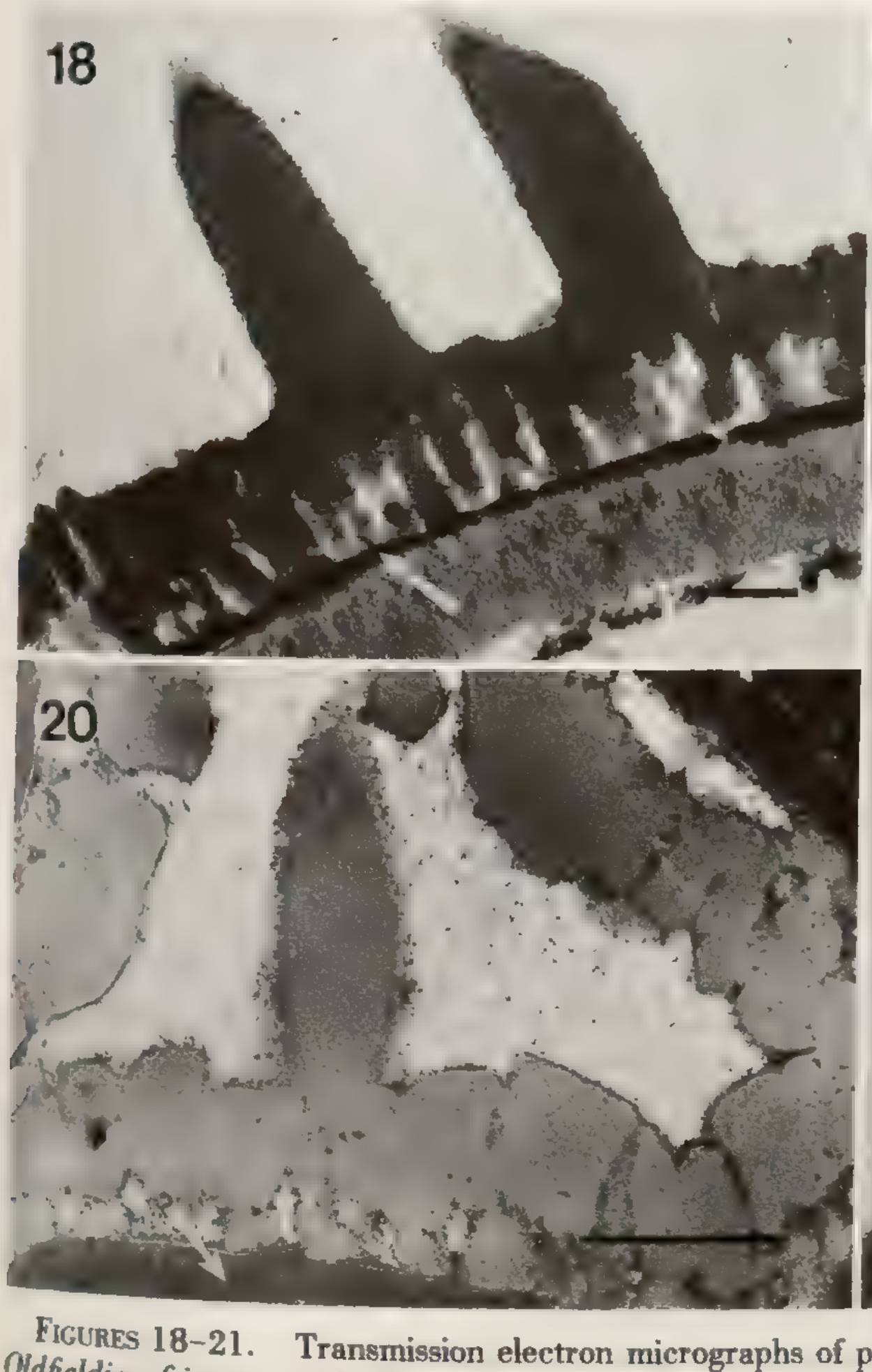


FIGURE 17. Distribution of pollen exine foot-layer thickness among sampled species of Euphorbiaceae. A circle (solid for species with the foot-layer homogeneous and open for species with the foot-layer irregular or absent) indicates the mean thickness, a vertical bar the range, and a rectangle two standard deviations on either side of the mean (N = minimum of 10 measurements from one to three grains). Species are arranged by increasing thickness within a subfamily, with the Phyllanthoideae on the left and the Oldfieldioideae on the right. Dashed lines separate size-classes that we considered potential character states. Abbreviations for species names: AMgu = *Amanoa guianensis*, AMst = *Amanoa strobilacea*, ANjo = *Androstachys johnsonii*, ANme = *Antidesma membranaceum*, ANve = *Antidesma venosa*, APfa = *Aporusa falcifera*, ARmo = *Aristogeitonia monophylla*, CEme = *Celaenodendron mexicanum*, CHma = *Choriceras majus*, CRna = *Croizatia naiguatensis*, DIba = *Dissiliaria baloghioides*, DIch = *Didymocistus chrysadenius*, DRla = *Drypetes lateriflora*, HYac = *Hymenocardia acida*, HYal = *Hyeronima alchorneoides*, HYgl = *Hyaenanche globosa*, HYul = *Hymenocardia ulmoides*, KAph = *Kairothamnus phyllanthoides*, LObu = *Longetia buxoides*, MAdi = *Margaritaria discoidea*, MIhe = *Micrantheum hexandrum*, MIze = *Mischodon zeylanicus*, NEba = *Neoroepera banksii*, NEbu = *Neoroepera buxifolia*, OLaf = *Oldfieldia africana*, PAma = *Parodiodendron marginivillosum*, PAsu = *Paradrypetes subintegrifolia*, PEpu = *Petalostigma pubescens*, PEqu = *Petalostigma quadriloculare*, PItr = *Piranhea trifoliata*, POlo = *Podocalyx loranthoides*, PSdi = *Pseudanthus divaricatissimus*, SCol = *Scagea oligostemon*, SEdu = *Securinega durissima*, STme = *Stachyandra merana*, STpo = *Stachystemon polyandrus*, STru = *Stachyandra rufibarbis*, TEdi = *Tetracoccus dioicus*, VOeu = *Voatamalo eugenioides*, WHte = *Whyanbeelia terrae-reginae*.

Longetia, Fig. 23). Finally, we interpreted the exine of *Amanoa guianensis* (Fig. 14) as lacking a tectum; the echinae of this taxon we believe to be homologous to columellae. Evidence for this interpretation is the different structure of these echinae (distally rounded, unlike all other investigated taxa, which have sharply pointed echinae) and the probable homology of the echinae of *Amanoa guianensis* with the columellae of the related *Amanoa strobilacea* (Fig. 15).

Tectum thickness varied considerably among the taxa we examined (Fig. 26). The variation was almost continuous, however, with the only supportable breaks associated with single taxa and therefore leading to phylogenetically uninformative autapomorphies if coded as separate states. We therefore did not use tectum thickness as a character.

10. Ektexinous periapertural thickenings. The pollen of most of the taxa we examined had much thicker exine around the apertures than in the nonapertural regions. In most cases these thickenings were formed by the endexine, but in a few genera the thickenings were formed by the ektexine; in no cases did we observe both endexinous and ektexinous thickenings. Occasional taxa had no apparent thick-



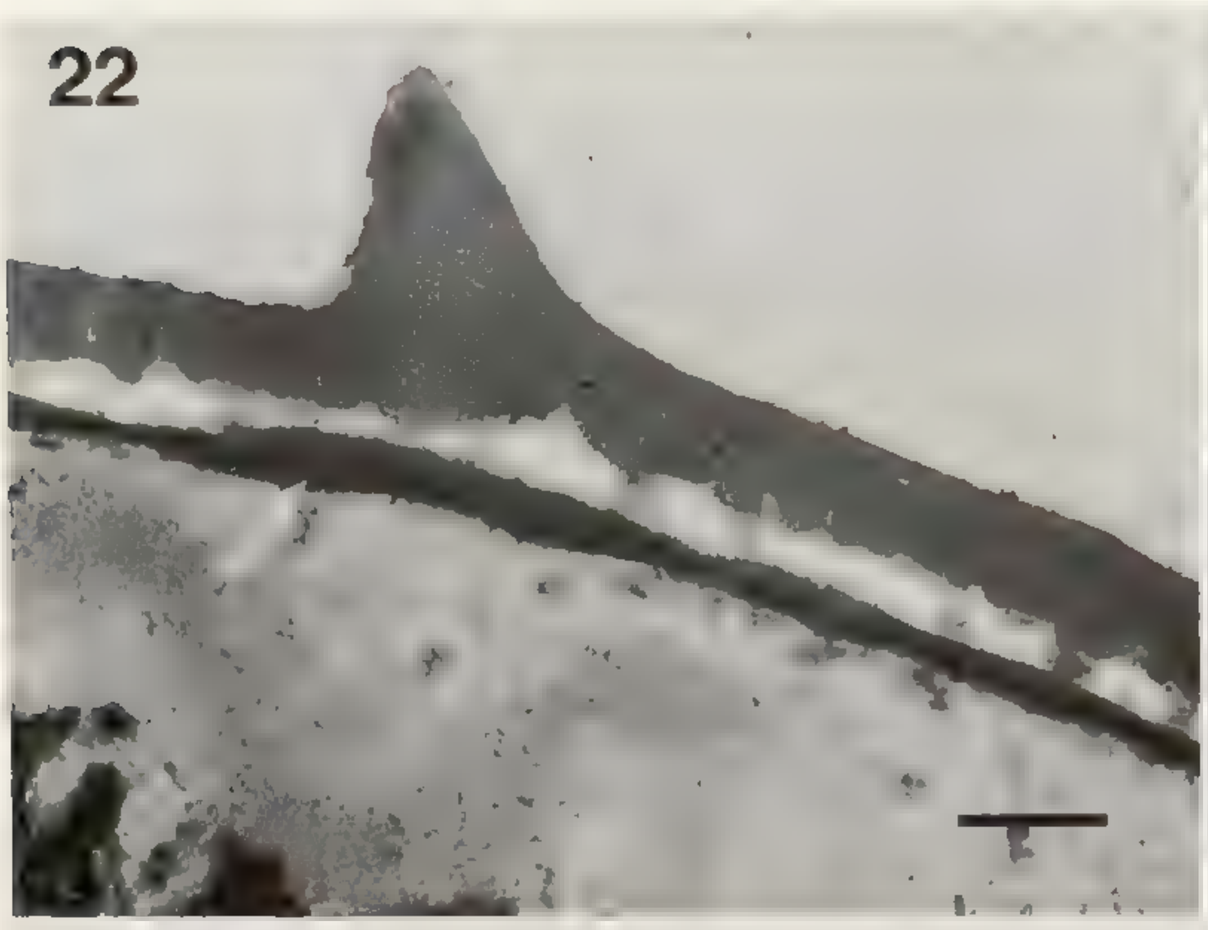
FIGURES 18–21. Transmission electron micrographs of pollen of Euphorbiaceae subfamily Oldfieldioideae.—18. *Oldfieldia africana*.—19. *Tetracoccus dioicus*.—20. *Podocalyx loranthoides*.—21. *Paradrypetes subintegrifolia*. Arrows indicate endexine. Scale bars = 0.5 μm.

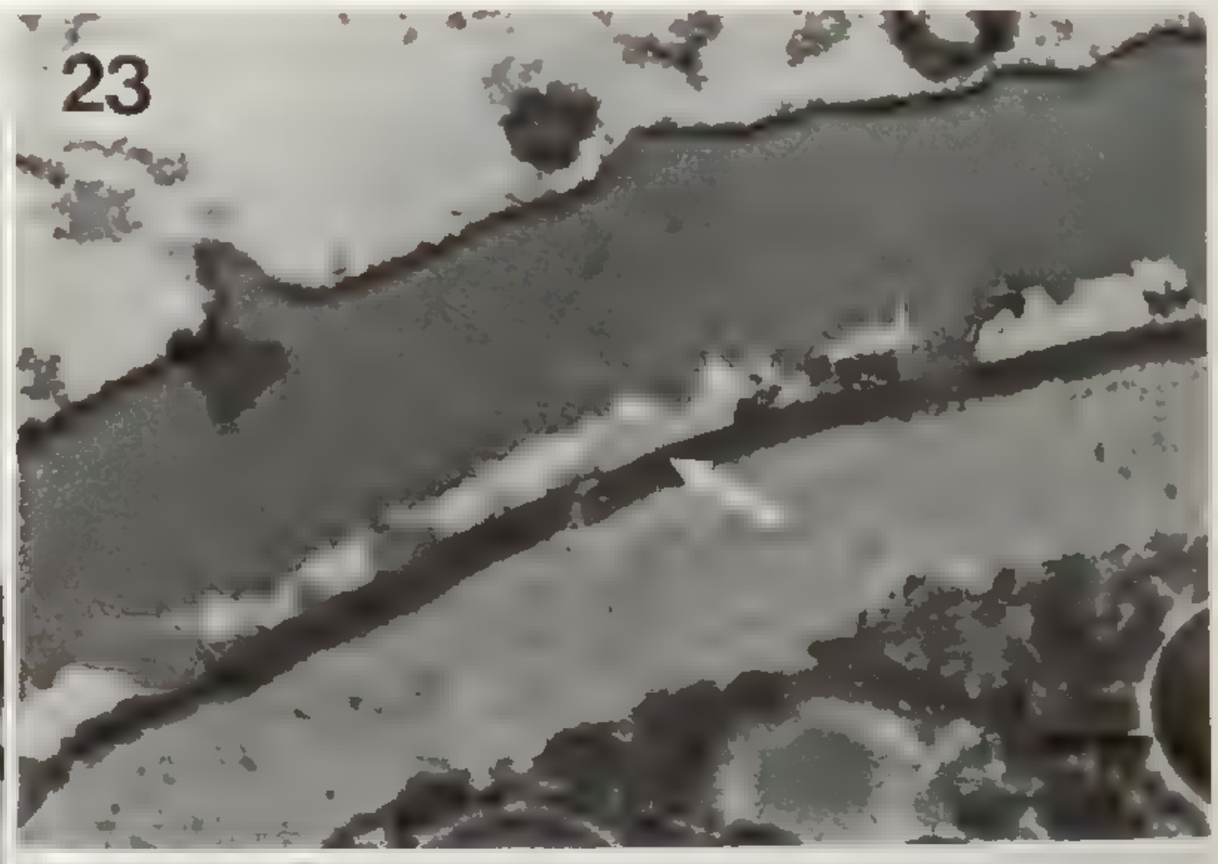
enings, though in several of these the endexine became more electron-dense around the apertures. Because preliminary analysis showed that the presence or absence of endexinous thickenings had little phylogenetic significance, we have included only ektexinous thickenings in this analysis.

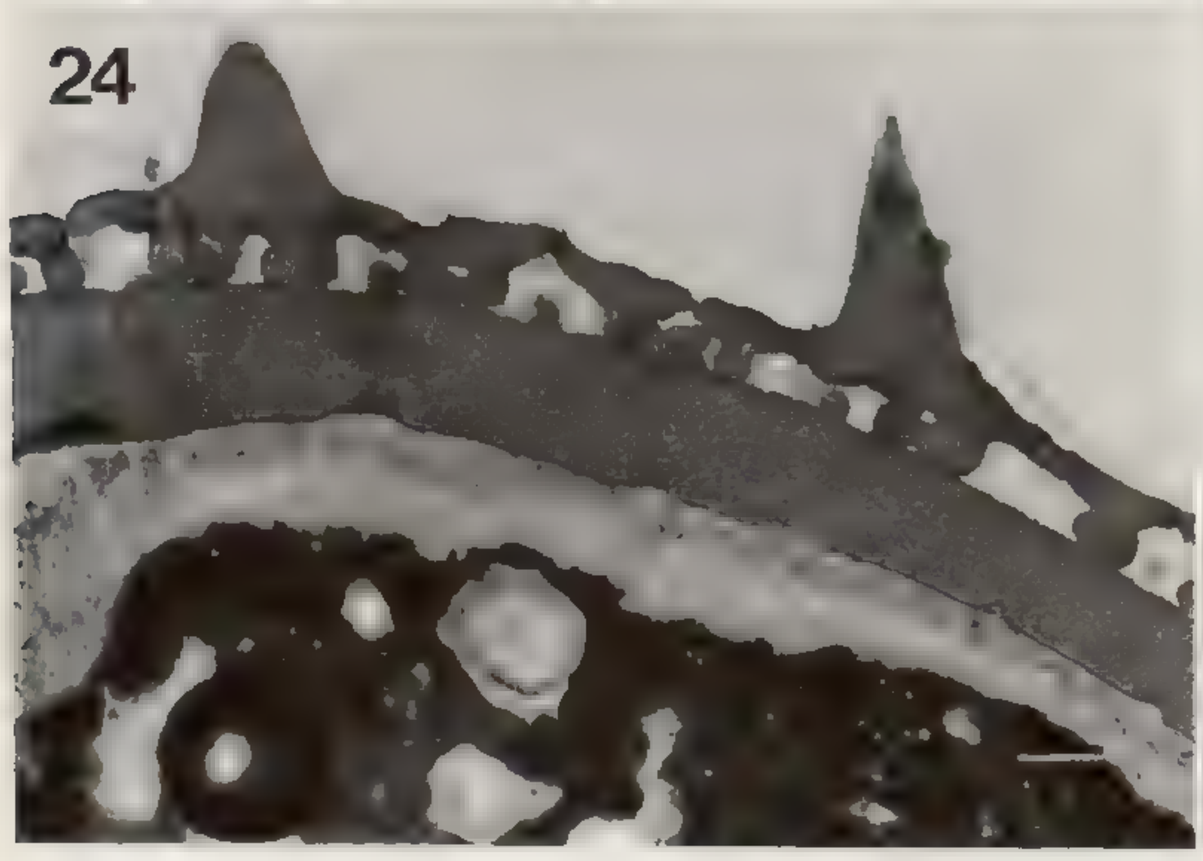
Alternative codings. Though the way in which we have coded the pollen characters may appear to permit them to vary independently, the pattern of variation within the taxa combined with the coding predisposes certain outcomes. This problem, and our attempt to address it, can be most easily demonstrated with the characters for aperture number and distribution. As we have coded these characters, a group potentially supported by the pan-aperturate condition is nested within a group potentially defined by aperture number greater than three; the group with more than three zonate apertures is necessarily paraphyletic based on these characters alone. This is because all taxa with pan-aperturate pollen, the derived state of one character, have more than three apertures, the derived state of another character. Combining these two characters into a single, unordered character with three states—zonate with three apertures, zonate with more than three apertures, and pan-aperturate—allows the group with more than three zonate apertures to be potentially monophyletic based on this single pollen character. We tried recoding these characters and found that both codings gave the same cladograms.

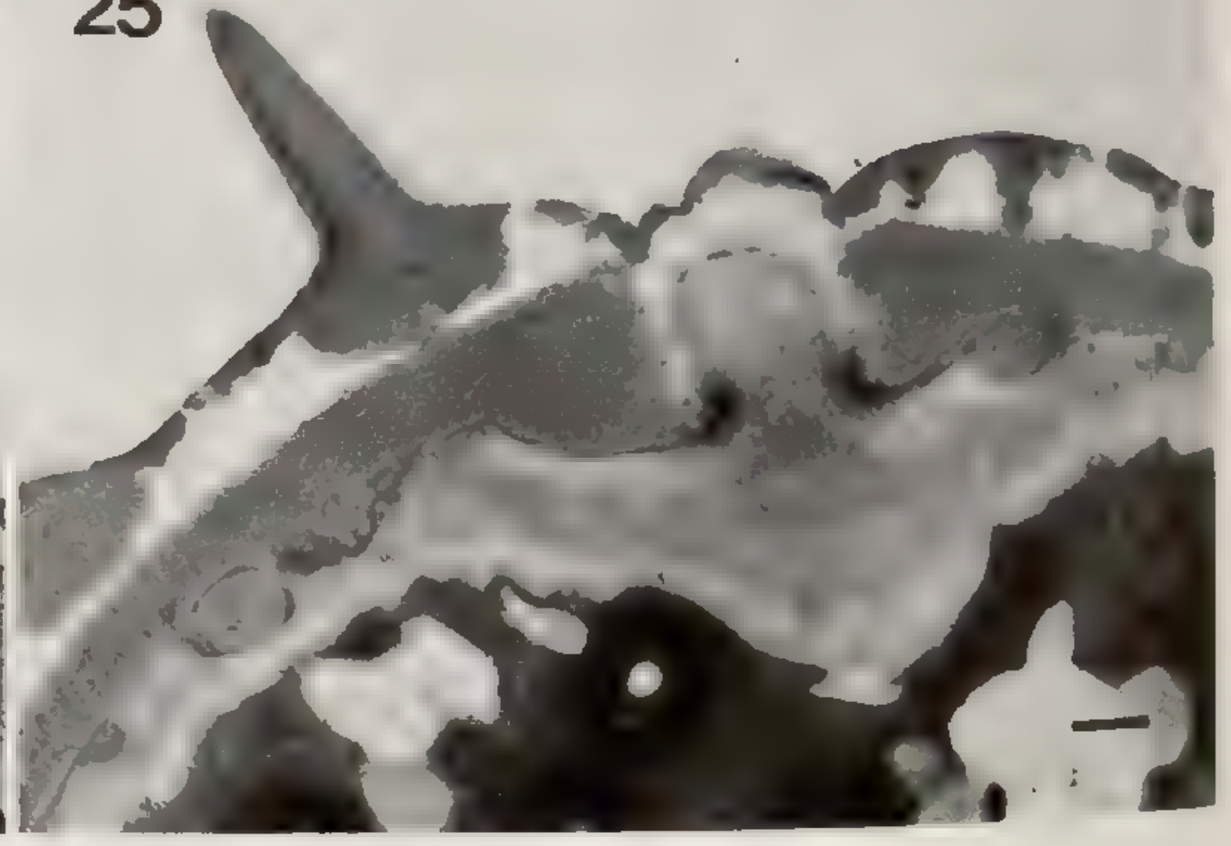
Similar considerations apply to pollen shape and aperture type, pollen shape and aperture number, and nonspinal sculpture and tectum structure, and perhaps others. As with the example we discussed above, combining a pair of characters into a one unordered multistate character did not affect the results of our phylogenetic analysis. We have therefore chosen to present the data as we have, which we consider simpler and more informative.

Vegetative morphology and anatomy. Most of the wood and leaf characters (11–47) that we included in our analysis are discussed by Hayden









FIGURES 22–25. Transmission electron micrographs of pollen of Euphorbiaceae subfamily Oldfieldioideae.—22. *Androstachys johnsonii.*—23. *Longetia buxoides.*—24. *Scagea oligostemon.*—25. *Stachystemon polyandrus.* Arrow in Figure 23 indicates endexine. Scale bars = 0.5 μm.

(1994, this issue). We obtained data for the Oldfieldioideae from his paper, and data for genera in Phyllanthoideae and the uniovulate subfamilies of Euphorbiaceae from Hayden (1980), Levin (1986a), Matos Araujo & Mattos Filho (1984), Mennega (1984, 1987), Metcalfe & Chalk (1950), Milanez (1935), and miscellaneous monographs cited below. In most cases, we could code characters directly from Hayden (1994). Following is a discussion of those characters he did not include or for which our interpretation may differ from Hayden's.

12. Perforation plates. Rather than distinguishing exclusively scalariform from mixed simple and scalariform, we combined these conditions into one state. Had we treated them as separate states, polarizing the character would have been difficult because both conditions are found within some of the genera of Phyllanthoideae we included as outgroups.
19. Crystalliferous ray cells. Many genera have ray cells containing one or occasionally several crystals. In most of these genera, as far as we can gather from the literature (e.g., Hayden, 1980, 1994; Milanez, 1935; Matos Araujo & Mattos Filho, 1984), the crystalliferous cells are unsclerified. In *Aristogeitonia*, *Mischodon*, *Voatamalo*, and the alternate-leaved species of *Tetracoccus*, however, the crystalliferous ray cells are sclerified. Unfortunately, ambiguities in the literature regarding wood anatomy of the Phyllanthoideae prevent us from being entirely confident about the condition of some of our outgroup genera.
20. Axial xylem parenchyma. Axial xylem parenchyma is uniformly present in the Oldfieldioideae, though its distribution varies to some extent. Only limited data on the distribution of axial xylem parenchyma are available for the Phyllanthoideae, so we were able only to record its presence or absence. Despite this extreme simplification, we included this character because it helps resolve relationships among

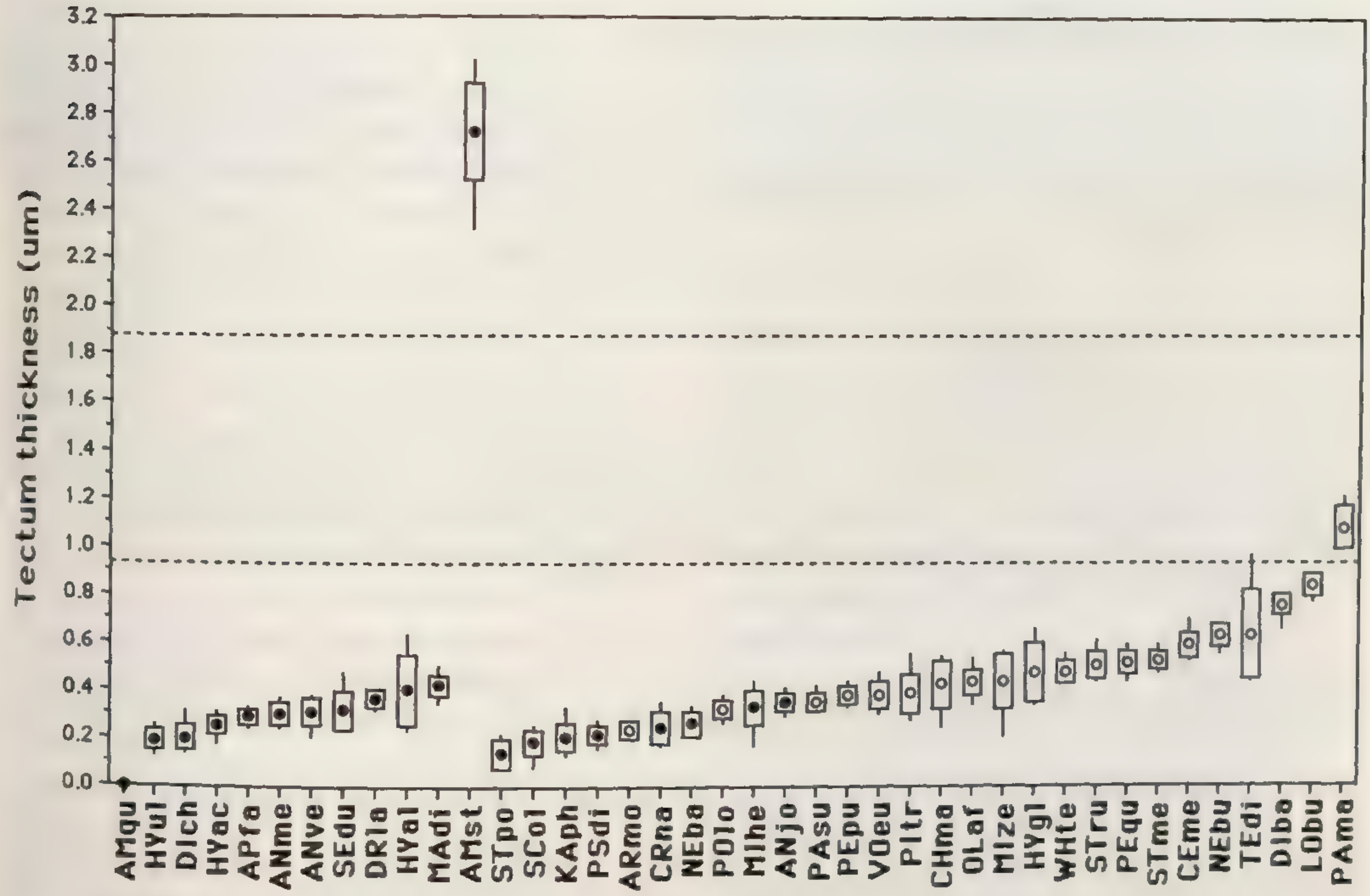


FIGURE 26. Distribution of pollen tectum thickness among sampled Euphorbiaceae. Format and abbreviations are the same as in Figure 17.

the taxa we included as outgroups for the Oldfieldioideae.

24. Leaf blade. We tried treating this character both as an unordered character and as an ordered character arranged simple to compound to unifoliolate. In our experience with other groups, unifoliolate leaves appear to be reductions from compound leaves rather than to have evolved directly from simple leaves. With this data set, we found that it is more parsimonious to derive unifoliolate leaves from compound leaves, regardless of whether the character is ordered or unordered. We coded *Micrantheum*, interpreted as having either sessile compound leaves or simple leaves with foliate stipules (Hayden, 1994), as equivocal ("?") for this character.

25. Phyllotaxy. We coded opposite and whorled as the same state because at least some species, e.g., *Tetracoccus dioicus*, bear both opposite and whorled leaves. Two genera, *Tetracoccus* and *Oldfieldia*, have some species with alternate leaves and others with opposite or whorled leaves. Because the phylogeny of species within these genera is not well understood, we coded these taxa as polymorphic for this character.

29. Stomatal pattern. Because Phyllanthoideae have both paracytic and brachyparacytic stomata, sometimes on the same leaf (Levin 1986a), we treated these as the same state. Though the only other stomatal pattern in Oldfieldioideae is anomocytic, *Aporusa*, one of the outgroup genera, has anisocytic stomata. We did not differentiate between undivided and subdivided subsidiary cells because this may vary within a single leaf (Hayden, 1994).

31. Phloem fibers of primary vein. In most genera the phloem fibers in the primary vein have thick lignified walls. In *Micrantheum*, *Neoroepera banksii*, *Pseudanthus*, and *Stachystemon*, the fibers are similarly thick-walled but unlignified. The phloem fibers of *Petalostigma* are also unlignified but have thin walls (W. J. Hayden, pers. comm.). Because of the difference in wall thickness, we were not sure a priori that the unlignified condition was homologous in these five taxa. We

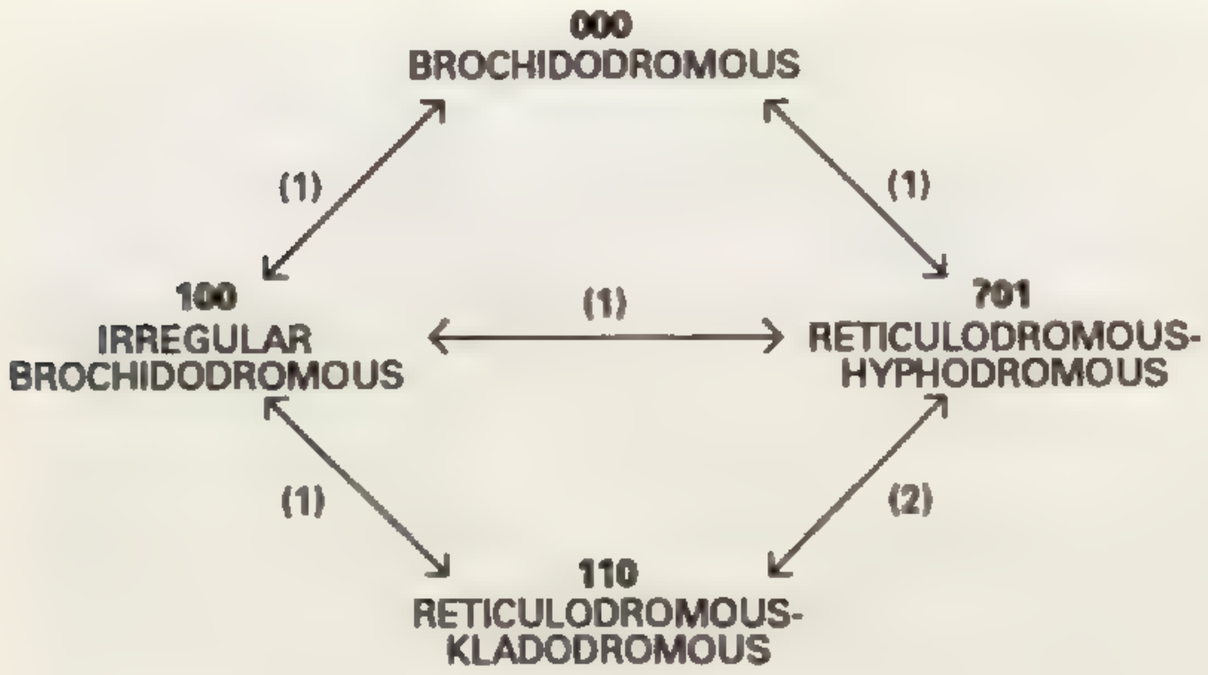


FIGURE 27. Character coding for leaf venation, characters 35–37.

therefore recognized three unordered states for the phloem fibers: lignified, thick-walled and unlignified, and thin-walled and unlignified.

34. Bundle sheath extension crystals. Some genera have no bundle sheath extensions (character 33, state 0). We coded these genera as equivocal ("?") for character 34.

35–37. Venation. Four basic leaf venation patterns occur in Oldfieldioideae (Hayden, 1980, 1994). In most genera venation is brochidodromous (coded 000 for these characters; terminology follows Hickey, 1979), but considerably less organized venation is found in four genera. The venation of *Micrantheum* forms a highly irregular brochidodromous pattern, which we coded "100." More irregular still is the reticulodromous to kladodromous venation of *Stachystemon* and *Pseudanthus*. Because the reticulodromous pattern in some *Stachystemon* species appears somewhat like the venation pattern in *Micrantheum*, we interpret irregular brochidodromous venation as evolutionarily intermediate to reticulodromous to kladodromous venation, and code the condition in *Stachystemon* and *Pseudanthus* "110." Finally, *Tetracoccus* leaves have reticulodromous to hyphodromous venation. It was not clear a priori whether this pattern evolved from irregular brochidodromous venation like that of *Micrantheum* or if it evolved independently from a brochidodromous pattern, but it probably did not evolve from kladodromy. To allow the two likely possibilities to be equally parsimonious a priori, we coded reticulodromous to hyphodromous venation "?01." See Figure 27 for a diagram of our proposed leaf venation transformation series and its coding.

45–46. Stipules. McPherson & Tirel (1987) stated that the stipules of *Austrobuxus* and *Longetia* are extremely reduced to absent. The same may be true of other Dissiliariinae sensu Webster (1994), but we cannot find specific reference to the stipules in the other genera in the subtribe and have therefore coded these genera as equivocal ("?"). When describing *Whyanbeelia*, Airy Shaw & Hyland (in Airy Shaw, 1976) stated "*stipulae haud certe visae, forsan obsoletae*" (stipules not certainly seen, perhaps obsolete). One of us (Levin) examined a paratype of *W. terrae-reginae* (*Hyland 3041*, DAV) and was unable to find evidence of stipules. We have therefore tentatively coded *Whyanbeelia* as lacking stipules (see further discussion in section on taxonomic implications). We coded *Micrantheum* as equivocal ("?") for this character; see the discussion of character 24 above.

In addition to stipule size, stipule position appeared phylogenetically significant. Stipules may arise from the stem or be epipetiolar, i.e., arise from the petiole.

47. Raphides. *Paradrypetes* is unique among Oldfieldioideae, and apparently Euphorbiaceae, in having raphides (Milanez, 1935; Matos Araujo & Mattos Filho, 1984; Levin, 1986a). All other Euphorbiaceae with crystals have druses and/or prismatic crystals.

Reproductive morphology. For completeness we tried to include some characters of reproductive morphology in our phylogenetic analysis. Unfortunately we have been completely dependent on published descriptions for genera other than *Paradrypetes*. Literature reports on reproductive morphology of Oldfieldioideae are incomplete and often difficult to interpret because different authors have used descriptive terms inconsistently. For example, floral discs in some genera are described as "fused glands" whereas in others they may be described as "lobed." Without first-hand experience with the flowers, we cannot tell whether discs in these genera are actually different or merely described differently. Inflorescence architecture is similarly difficult to interpret. When we restricted our list to those characters we felt we could interpret with reasonable confidence, only five characters (48–52) remained. We expect that a careful study of

oldfieldioid reproductive morphology will yield significant characters beyond those in our meager list.

Following is a discussion of each of the reproductive characters we included. We obtained most of our data on reproductive morphology from Pax & Hoffmann (1922, 1931), Bosser (1976), Airy Shaw (1972, 1974, 1976, 1980), and McPherson & Tirel (1987).

48. Sexuality. Plants may be either monoecious or dioecious. The literature was unambiguous regarding the character state in each genus except *Aristogeitonia*. Pax & Hoffmann (1931) described this genus as monoecious, but both Airy Shaw (1972) and Radcliffe-Smith (1987b) reported it to be dioecious. We have followed the more recent authors who worked with far more specimens.
49. Petals. Though petals are uniformly absent in the Oldfieldioideae, we included this character to help resolve relationships among the outgroup taxa.
50. Ovules/locule. Since Jussieu (1824) first recognized its importance, ovule number has been regarded as one of the principal taxonomic characters in Euphorbiaceae. Phyllanthoideae and Oldfieldioideae bear two ovules/locule, whereas the remaining Euphorbiaceae bear one ovule/locule. *Scagea*, however, is uniovulate (McPherson, 1985; McPherson & Tirel, 1987) yet has pollen like that of some Oldfieldioideae (Simpson & Levin, in prep.; see also the cladistic analysis below).
51. Caruncle on seeds. Most Oldfieldioideae have carunculate seeds. Apparent exceptions are *Androstachys* (Dahlgren & van Wyk, 1988), *Aristogeitonia* (Pax & Hoffmann, 1922; Radcliffe-Smith, 1987a), *Celaenodendron* (Standley, 1927), *Kairothamnus* (Airy Shaw, 1974, 1980), and *Picrodendron* (Hayden, 1977; Hayden et al., 1984). We were unable to find data on *Neoroepera*, *Podocalyx*, *Voatamalo*, and *Whyanbeelia*.
52. Endosperm. With the exception of *Hyaenanche* (Pax & Hoffmann, 1922) and *Picrodendron* (Hayden, 1977; Hayden et al., 1984), Oldfieldioideae have seeds with abundant endosperm. We were unable to obtain data on *Kairothamnus*, *Voatamalo*, and *Whyanbeelia*.

CHARACTER POLARIZATION

Phylogenetic analysis of the primitive Euphorbiaceae is complicated by the absence of a clear consensus regarding the relationships of the family (see review by Webster, 1987) and therefore which taxa should be chosen as outgroups to polarize the characters. Taxa that have been proposed in recent years include Flacourtiaceae (Hickey & Wolfe, 1975; Levin, 1986a, c), Celastrales (Cronquist, 1981), Linales (Webster, 1987), and Malvales, particularly Elaeocarpaceae and Sterculiaceae (Takhtajan, 1980; Dahlgren, 1983; Thorne, 1983). In the absence of a well-accepted outgroup, particularly when the potential outgroups appear not to be closely related to each other, as is clearly the case here, the best approach may be the outgroup substitution method proposed by Donoghue & Cantino (1984; see also Maddison et al., 1984). In this method, the potential outgroups are used alone and in plausibly related groups in separate phylogenetic analyses. The resulting cladograms are then examined for regions of consensus. In our analyses, we used each outgroup separately, Elaeocarpaceae plus Sterculiaceae (Malvales), Flacourtiaceae plus Elaeocarpaceae plus Sterculiaceae (Dilleniidae of Cronquist, 1981), Linales plus Flacourtiaceae (Chase et al., 1991; M. Chase, pers. comm.), and all outgroups together without any predetermined topology.

CLADISTIC ANALYSIS

Table 3 contains the character × taxon data matrix for our analyses. In order to explore the systematic implications of the pollen data we first performed cladistic analyses on these data alone. Then we performed cladistic analyses on the complete data set. In both cases both PAUP and HENNIG86 yielded numerous equally parsimonious trees, differing mainly in local rearrangement of taxa. We therefore produced a strict consensus tree for each data set. Choice of outgroup did not change the topology of the Oldfieldioideae on the consensus trees, but did affect the topology of the remaining taxa enough that a consensus among the various trees has limited resolution. Because of this and our limited sample of non-oldfieldioid taxa we will restrict most of our discussion to the relationships among Oldfieldioideae.

Pollen. Initial analysis showed that nonspinal sculpturing (character 6) was very homoplastic. Because of this and the large number of taxa for which we were unable to determine the sculpturing, we dropped this character from further analysis. The consensus tree based on the remaining pollen data alone is shown in Figure 28. We show only the Oldfieldioideae (including *Croizatia*, *Paradrypetes*, and *Scagea*); the tree is rooted using the

TABLE 3. Character × taxon matrix for cladistic analysis of investigated Euphorbiaceae. All multistate characters are unordered. A "?" indicates an unknown or equivocal character state. Taxa with polymorphic characters are indicated by an "&" preceding a second line containing the alternate states for the polymorphic characters. Outgroup taxa are listed first, followed by taxa in the Euphorbiaceae. Taxa in the Phyllanthoideae are listed alphabetically, whereas taxa in the Oldfieldioideae are in the order shown in one of our preferred cladograms (Figs. 31 33A).

Taxa	Characters 000000000111111111122222222223333333333444444444455 123456789012345678901234567890123456789012345678901234567890123456789012
Outgroups	
Flacourtiaceae	00000??00?0????00?010??000???00?0?0000??0?0000010000
Celastraceae	000000??0?0110?0010???00?0???000?00000??0?000001?0?0
Linales	?000????0??1??000??000?00?0?000???0000??0?0000010?11
Elaeocarpaceae	100000??0?00?1100?00?000000?0000??0000?10?00000?0000
Sterculiaceae	0?????????0110000?00000?000?1000??0000?10?00000??0?0
Euphorbiaceae	
Acalyphoideae	?0000??0??011?000??0?000??0?00???????0??0?00000??1?0
Crotonoideae	?000?0000?011?0001?0?00??10?00???????0??0?00000??1?0
Euphorbioideae	?00000?0??011?0001?0?000?10?00???????0??0?00000?11?0
Phyllanthoideae	
Amanoa strobilacea	00000000000010000?0000000?0000?0??000000000000010001
Amanoa guianensis	0000??005000100000?0000000?0000?0??000000000000010001
Antidesma	10000000000110100000?000000100?0??00000100000000001000
Aporusa	00000000000010000000?00000020?0??00000100000000001000
Didymocistus	000012000000?0100?01??000?0000?0??00000101000000100?
Drypetes	10000000000?10000?0000000?0100000000000?10?0000001000
Hyeronima	10000000000?0000000?000000000?0??00000100000000001000
Hymenocardia	00011200010110100001?000000000?0??00000101000000001001
Margaritaria	1000000000001?0100101?0000?0000?0??0000?100000000001000
Phyllanthus	????00000?0110100101?000000000?0??00000100000000011000
Securinega	00002?000001100001001??000?0?00?????????????????0000100?
Oldfieldioideae	
Croizatia	000121113 1??????????000?0000?0??00000100000000000001
Paradrypetes	0101242240000000000010001000000??000000000000101000
Podocalyx	0101242220000100000010000100100010000000011000001 0?0
Tetracoccus	0101232 12?1110000100000010000000??010000000?0001010
&	1 0
Parodiodendron	0101232120011110010000020000000111000000010000001 0?0
Picrodendron	0101232120011100010000 1?0000001110000101100000001001
Piranhea	0101232 12?0111000100000101010001110000111100000001010
Celaenodendron	01012?2120011100010000010101000111000010110 0?0001000
Oldfieldia	0101232120011000010000010000000010000010010 0?0001010
&	1
Androstachys	0111240010011000010000021000000010000010110101001010
Stachyandra	0101242110011000010000011000000010000010110101000000
Voatamalo	01012?212?0110000110 00?01????????0000?????0100 10??
Mischodon	01012?212?0110000110000011000000100000100100010010 10
Aristogeitonia	01012?21200110?0011000010101000 00?0000100100010010 00
&	2
Hyaenanche	0101232120011000000000001000010 00?0000000000000101 1
Austrobuxus	01012121 2?0111000000000010100100 0?0000000001000101 0
Whyanbeelia	01012121210110000000100010100100 0?0000000001001 10??
Longetia	0101142141?????????????0010100100100000000000100110 10
Choriceras	0101142111011000100000001010010 00?0000000010011010
Dissiliaria	01012?212101100000000000010110100 1?0000100100100010 10
Petalostigma	01012?21200110000000100000100120110000000000000001010
Neoroepera buxifolia	01112121 2?0110010100100000100100 0?0000000000011 0?0
Kairothamnus	0111211130?????????????0001001000?0000000000?001100?

TABLE 3. Continued.

Taxa	Characters 00000000011111111112222222222333333333344444444455 12345678901234567890123456789012345678901234567890123456789012
Scagea	01112111300000000000000000000000000000000000000000000000000
Neoroepera banksii	01112?113001100101001000001001100?0001000000000110?0
Micrantheum	01112111300110010100111?001001100?1001000000?0011010
Pseudanthus	01112111300110010100111000100110?1101000000000011010
Stachystemon	01112?0130??????????0??10001001100?1101000000000011010

remaining outgroup taxa (Table 3). The entire tree (with all the taxa in Euphorbiaceae we included) has a length of 34 steps and a consistency index (C.I.) of 0.47. The portion of the tree including just the Oldfieldioideae, as shown in Figure 28, is 24 steps long and has a C.I. of 0.62.

Though large portions of the tree are unresolved (as would be expected with only eight characters), our pollen data show several significant synapomorphies. As previously noted by Punt (1962, 1987), Köhler (1965), Webster (1975, 1994), and Hayden et al. (1984), Oldfieldioideae pollen is echinate (5: 2; character number: state number from Table 2) and has apertures that are brevicolporate to pororate to porate (4: 1) and greater than three in number (2: 1). It was these characteristics that initially prompted Köhler (1965) and Webster (1975) to recognize the subfamily. When Kuhlmann (1935) described *Paradrypetes* he allied it with *Drypetes* Vahl in Phyllanthoideae. Hutchinson (1969) was the first to place *Paradrypetes* with genera now placed in Oldfieldioideae, presumably because of its opposite leaves; these pollen data offer clear support for his innovation. *Scagea*,

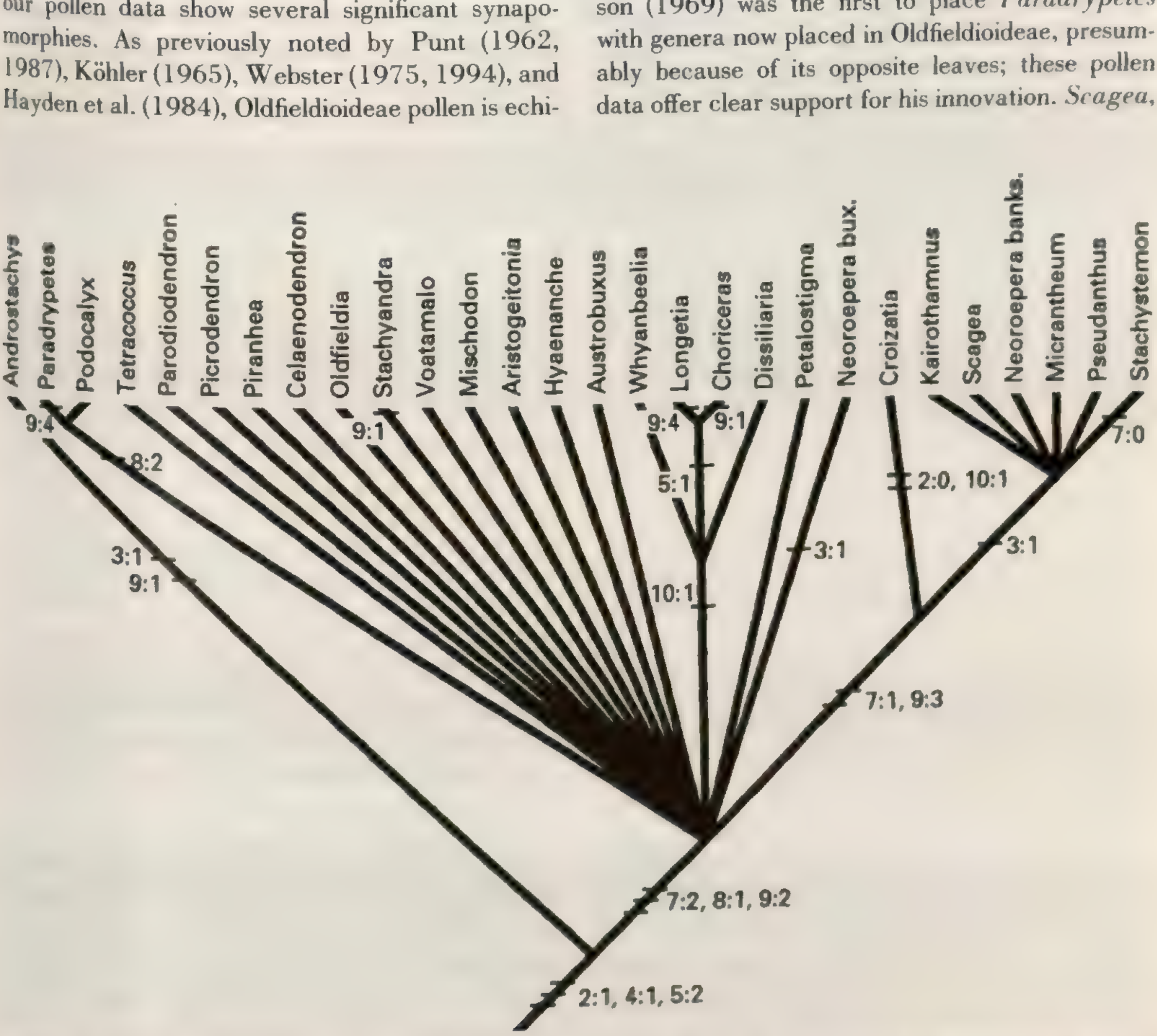


FIGURE 28. Strict consensus cladogram of the Oldfieldioideae based on palynological characters (1–5, 7–10) alone. In this and the following cladograms character state changes are shown by the character number, a colon, and the number ot the derived state (see Table 2).

too, shares these synapomorphies. Note that though *Croizatia* is well nested within the Oldfieldioideae, it has only three apertures (2: 0). *Securinega* also has echinate pollen, but has three colporate apertures (2: 0, 4: 0); it also lacks other synapomorphies shared by the Oldfieldioideae (see below). It would appear then that echinate sculpture is convergent in *Securinega* and the genus should remain in the Phyllanthoideae. Whether the oblate to globose shape is apomorphic or plesiomorphic for Oldfieldioideae cannot be resolved with our data.

Based on pollen alone, *Androstachys* would appear to be the sister group of the rest of the Oldfieldioideae and not to be closely related to *Stachyandra*. Three ultrastructural features appear to be synapomorphies of the rest of the subfamily: the foot-layer is irregular or absent (7: 2), the columellae are discontinuous with the foot-layer where it is present (8: 1), and the tectum is microperforate/baculate (9: 2). This last state was first recognized by Hayden et al. (1984) who examined *Austrobuxus* and *Picrodendron*. The pollen characters we used are remarkably uniform among most of the subfamily, hence the large polychotomy at this level in the tree.

Palynological characters allow recognition of several multigeneric clades at this level. The first clade, consisting of *Paradrypetes* (Fig. 21) and *Podocalyx* (Fig. 20), is united on the basis of their having the interstitium reduced or absent (8: 2). Because we treated the interstitial character as unordered, it is almost equally parsimonious to treat this state as synapomorphic for the entire subfamily and thus symplesiomorphic for these two genera. In that case, having columellae discontinuous with the foot-layer would be synapomorphic for the remaining genera of Oldfieldioideae. However, all the genera in Phyllanthoideae that we examined have a well-developed interstitium consisting of columellae that are continuous with the foot-layer, so it is more parsimonious to interpret the reduction of the interstitium as apomorphic.

The second clade, consisting of *Choriceras*, *Dissiliaria*, *Longetia* (Fig. 23), and *Whyanbeelia*, is defined by the presence of ektexinous periapertural thickenings (10: 1). Within this clade, *Choriceras* and *Longetia* form another clade, sharing reduced spines less than 1 μm long (5: 1); it is easy to understand why Punt (1962) and Köhler (1965), using only LM, described the pollen of these genera as psilate. The tectum in *Choriceras*, which is microperforate/homogeneous (9: 1), may actually be transitional between the microperforate/baculate condition and the imperforate tectum (9: 4) of *Longetia*.

Another clade, consisting of *Croizatia* (Fig. 16), *Kairothamnus*, *Scagea* (Fig. 24), *Neoroepera banksii*, *Micrantheum* (Figs. 9, 10), *Pseudanthus* (Figs. 11, 12), and *Stachystemon* (Fig. 25), shares a thick, homogeneous foot-layer (7: 1), first noted by Köhler (1965), and a microperforate/granular tectum (9: 3). *Croizatia* is the sister group of the remaining taxa, all of which share pantoporate apertures (3: 1). On this basis, *Neoroepera*, *Micrantheum*, *Pseudanthus*, and *Stachystemon* were previously recognized as a group by Punt (1962), Köhler (1965), and Webster (1975), who united them in the Pseudanthinae (*Kairothamnus* and *Scagea* had not yet been described). As previously noted by Köhler (1965), *Neoroepera buxifolia* (Figs. 3, 4), though pantoporate, has the exine structure typical of most Oldfieldioideae and therefore lacks the synapomorphies that place *N. banksii* in this clade. In all the equally most parsimonious trees, the pantoporate condition in *Androstachys* is convergent with the pantoporate condition in both this clade and *Neoroepera buxifolia* (cf. Fig. 28).

Combined character set. As might be expected given the greater number of characters, cladistic analysis of the entire data set yielded much better resolution of relationships. We again dropped pollen nonspinal sculpturing (character 6) from the analysis because of its relatively high homoplasy and our difficulty in determining the character states of many taxa (but see further discussion of this character below). Several hundred equally parsimonious trees resulted. We did not search the sets of trees resulting from different choices of outgroups for duplicate cladograms so we cannot state the precise number of equally parsimonious trees. We did compare the clade consisting of the Oldfieldioideae, however, and found 24 equally parsimonious arrangements of these taxa. Figure 29 illustrates the strict consensus tree for the relationships among the taxa of Euphorbiaceae we included and Figure 30A shows the strict consensus tree for the Oldfieldioideae. The trees including all the Euphorbiaceae taxa are 128 steps long (C.I. = 0.47) if all characters are included, or 124 steps long (C.I. = 0.45) if the autapomorphies are excluded. The 24 trees including just the Oldfieldioideae are 104 steps long (C.I. = 0.54) if all characters that vary among these taxa are included, or 97 steps long (C.I. = 0.50) if autapomorphies are excluded. Cladistic analysis of the data from vegetative morphology and anatomy data alone (taken from Hayden, 1994) yielded similar but less resolved trees.

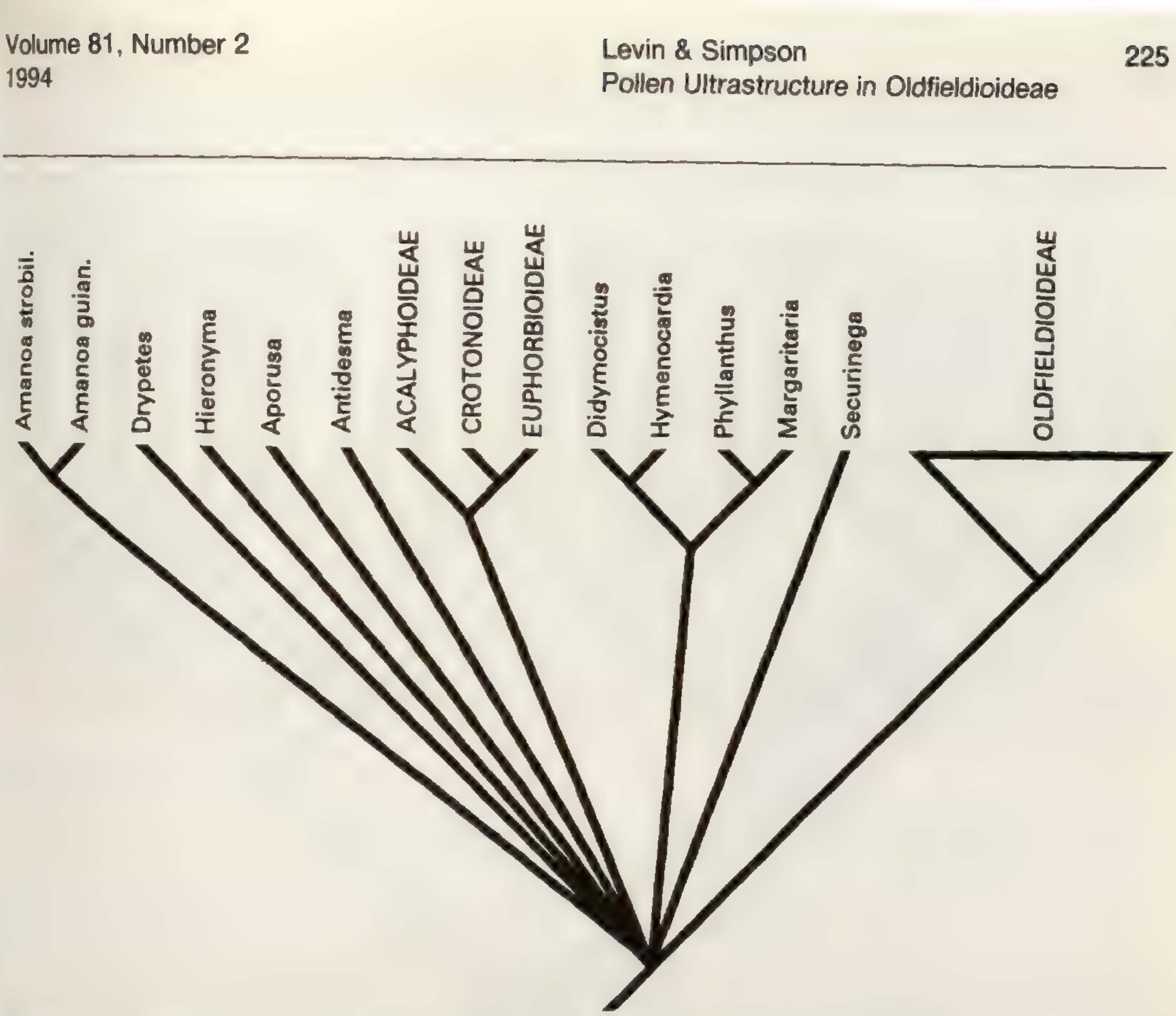


FIGURE 29. Strict consensus cladogram of the taxa of Euphorbiaceae included in our study, based on palynological, vegetative, and reproductive characters (1–5, 7–52). Names in all capital letters are of subfamilies. The phylogeny of the Oldfieldioideae, represented here by a triangle, is shown in Figure 30.

The polychotomy in clade A of Figure 30A is a consequence of the polymorphism in phyllotaxy (character 25) found in *Oldfieldia*; the trichotomy and both dichotomous resolutions are equally parsimonious. Accepting this polychotomy as unresolvable reduces the number of substantially different equally parsimonious cladograms for the Oldfieldioideae to eight. A fundamental difference among these eight cladograms is the placement of *Tetracoccus* and the clade consisting of *Paradrypetes* and *Podocalyx*. Three different arrangements are equally parsimonious (Fig. 30B–D). All but the three cladograms with the basic arrangement shown in Figure 30B require two reversals that we consider unlikely: derivation of scalariform perforation plates from simple perforation plates (character 12) and derivation of transitional intervascular pitting from alternate intervascular pitting (character 13). The vessels of both genera of Oldfieldioideae known to have scalariform perforation plates and transitional intervascular pitting, *Paradrypetes* and *Podocalyx*, are about 1.0–1.4 mm long, much longer than those of other Oldfieldioideae, which are typically about 0.3–0.4 mm long (Hayden, 1980; Matos Araujo & Mattos Filho, 1984), which is consistent with the interpretation that these character states are plesiomorphic. These three cladograms differ only in the relative positions of *Austrobuxus*, *Dissiliaria*, *Hyaenanche*, *Petalostigma*, *Whyanbeelia*, and the clade consisting of *Choriceras* plus *Longetia* within clade B of Figure 30. Two of these three cladograms are also those obtained using the successive weighting method of Farris (1969), which weights characters with low homoplasy greater than those with high homoplasy. These two cladograms, which we prefer because they do not require improbable reversals and are better supported by what we consider the more reliable characters (those with low homoplasy) are shown in Figures 31–33. (The third cladogram, not shown, is similar to Fig. 33A but with *Hyaenanche* the sister group of the clade consisting of *Austrobuxus*, *Choriceras*, *Dissiliaria*, *Longetia*, and *Whyanbeelia*.) In contrast to the polychotomy involving *Oldfieldia* (Figs. 30A and 32), the polychotomies shown in Figure 33 result from absence of synapomorphies (zero branch lengths) rather than character conflicts and therefore cannot be further resolved with our data.

The trees produced using pollen data alone (e.g., Fig. 28) are almost entirely consistent with our preferred trees produced using all the data (Figs.

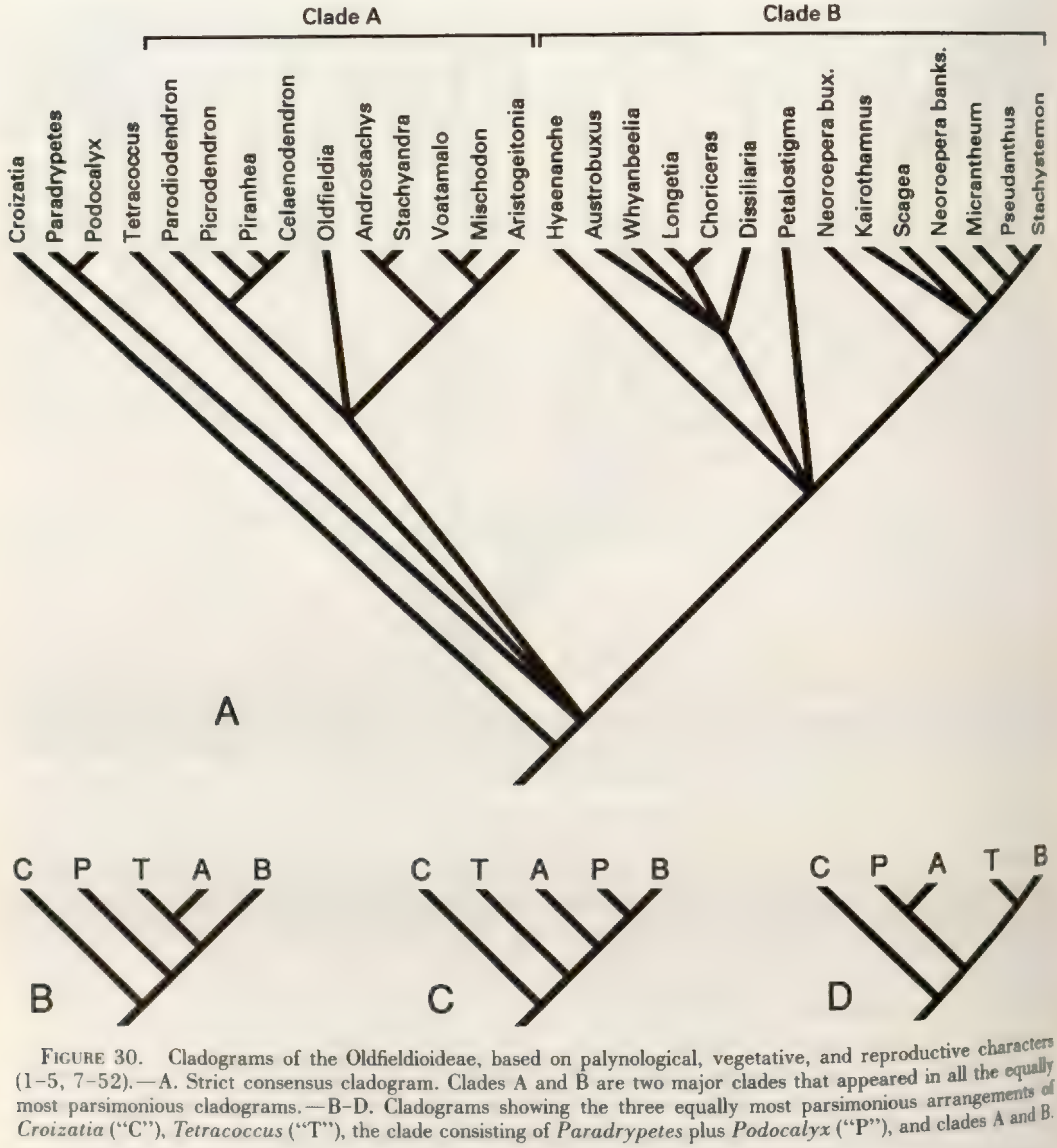


FIGURE 30. Cladograms of the Oldfieldioideae, based on palynological, vegetative, and reproductive characters (1–5, 7–52).—A. Strict consensus cladogram. Clades A and B are two major clades that appeared in all the equally most parsimonious cladograms.—B–D. Cladograms showing the three equally most parsimonious arrangements of *Croizatia* ("C"), *Tetracoccus* ("T"), the clade consisting of *Paradrypetes* plus *Podocalyx* ("P"), and clades A and B.

31–33). The two exceptions are the positions of *Androstachys* and *Croizatia*. Instead of being basal, as in the pollen-based cladogram (Fig. 28), *Androstachys* forms a clade with *Stachyandra*, to which it certainly is closely related (Radcliffe-Smith, 1990). This relationship is supported by three synapomorphies: microperforate/homogeneous tectum (9: 1), foliar veins beyond the tertiaries indistinguishable in a reticulum (41: 1), and the presence of columnar foliar sclereids (44: 1); in addition, these genera share rather unusual floral morphology, notably the staminate inflorescences which consist of a triad of flowers, each with numerous stamens borne on an elongate androphore (Airy Shaw, 1970; Dahlgren & van Wyk, 1988; Radcliffe-Smith, 1990). In turn, a sequence of morphological synapomorphies (notably circular and alternate vessel-ray pits (18: 1), compound or unifoliolate leaves (24: 1, 2), well-developed bundle sheath extensions (33: 1), fimbriate marginal ultimate venation (39: 1), well-developed areoles (42: 1), and epipetiolar stipules (46: 1)) cause *Androstachys* and *Stachyandra* to be nested well up within the Oldfieldioideae (Figs. 31, 32). Placing *Androstachys* at the base of the subfamily, as shown in Figure 28, increases the length of the combined data set tree by at least nine steps, and placing *Androstachys* and *Stachyandra* together at the

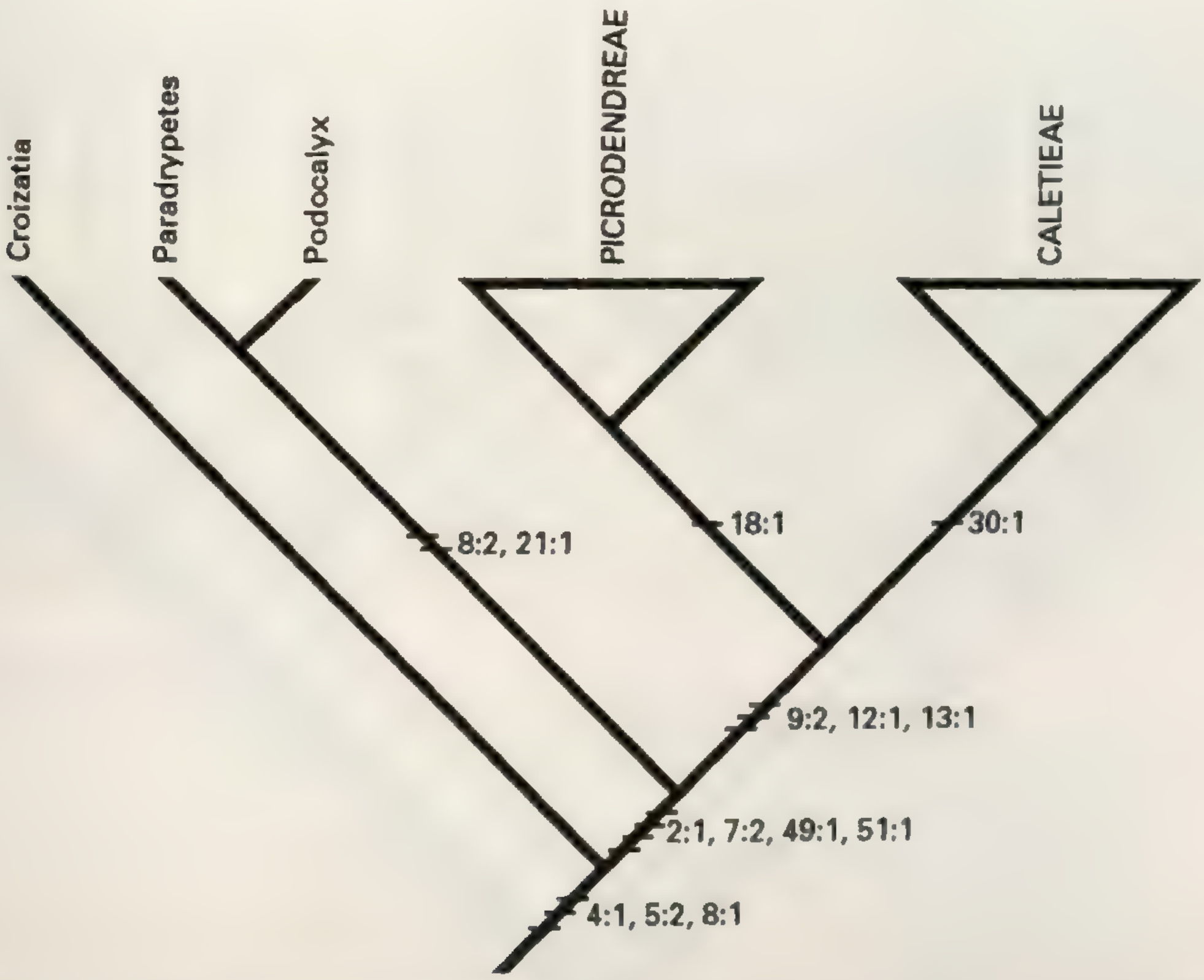


FIGURE 31. Preferred most parsimonious cladogram of the Oldfieldioideae based on palynological, vegetative, and reproductive characters (1–5, 7–52). Triangles represent tribes whose subtribal relationships are shown in Figures 32 and 33. Only synapomorphies are shown, so some characters are more homoplastic than indicated.

FIGURE 32. Preferred most parsimonious cladogram of Oldfieldioideae tribe Picrodendreae based on palynological, vegetative, and reproductive characters (1–5, 7–52). Only synapomorphies are shown, so some characters are more homoplastic than indicated.

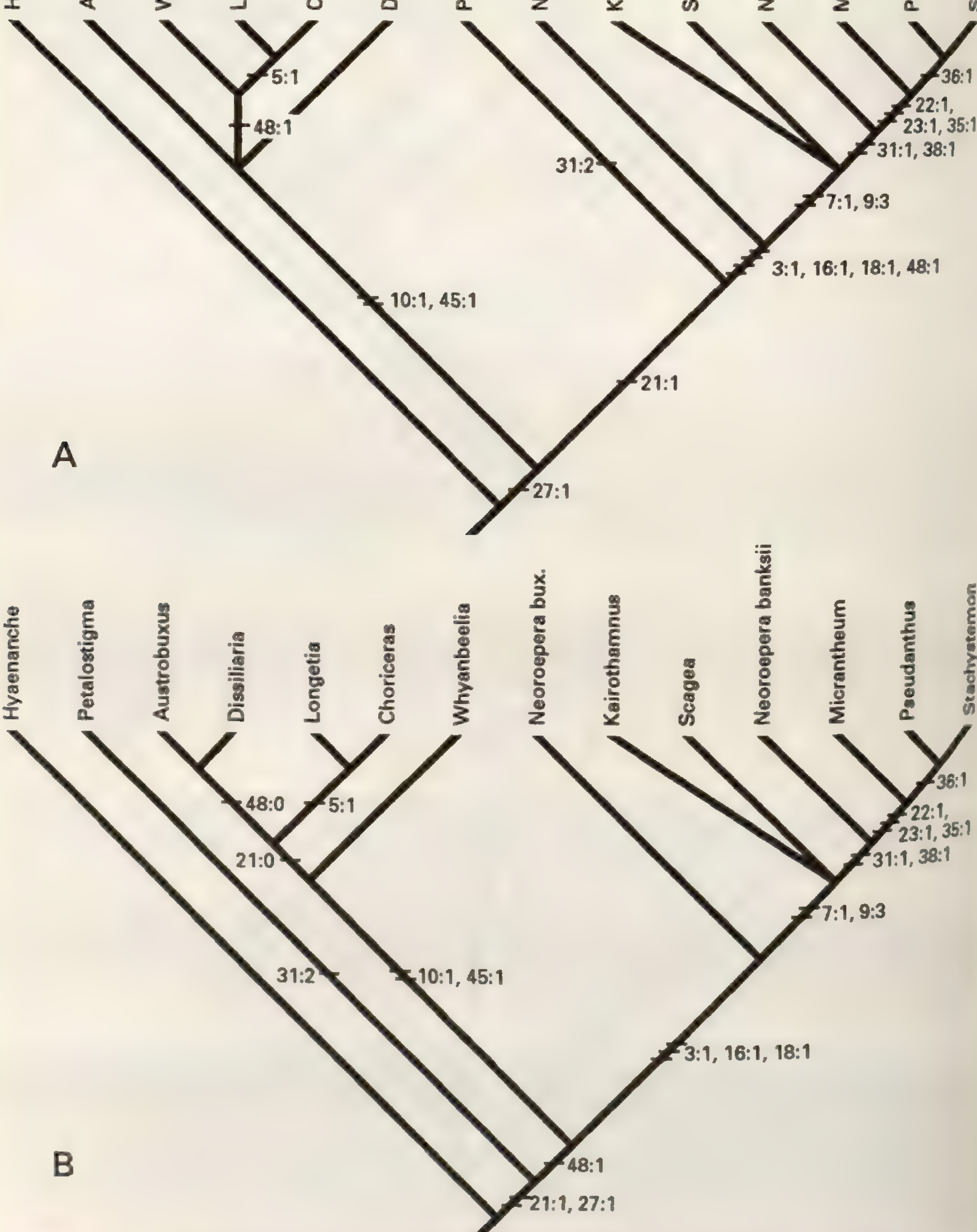


FIGURE 33. The two preferred most parsimonious cladograms (A, B) of Oldfieldioideae tribe Caletieae based on palynological, vegetative, and reproductive characters (1–5, 7–52). With the exception of character 31, only synapomorphies are shown, so some characters are more homoplastic than indicated.

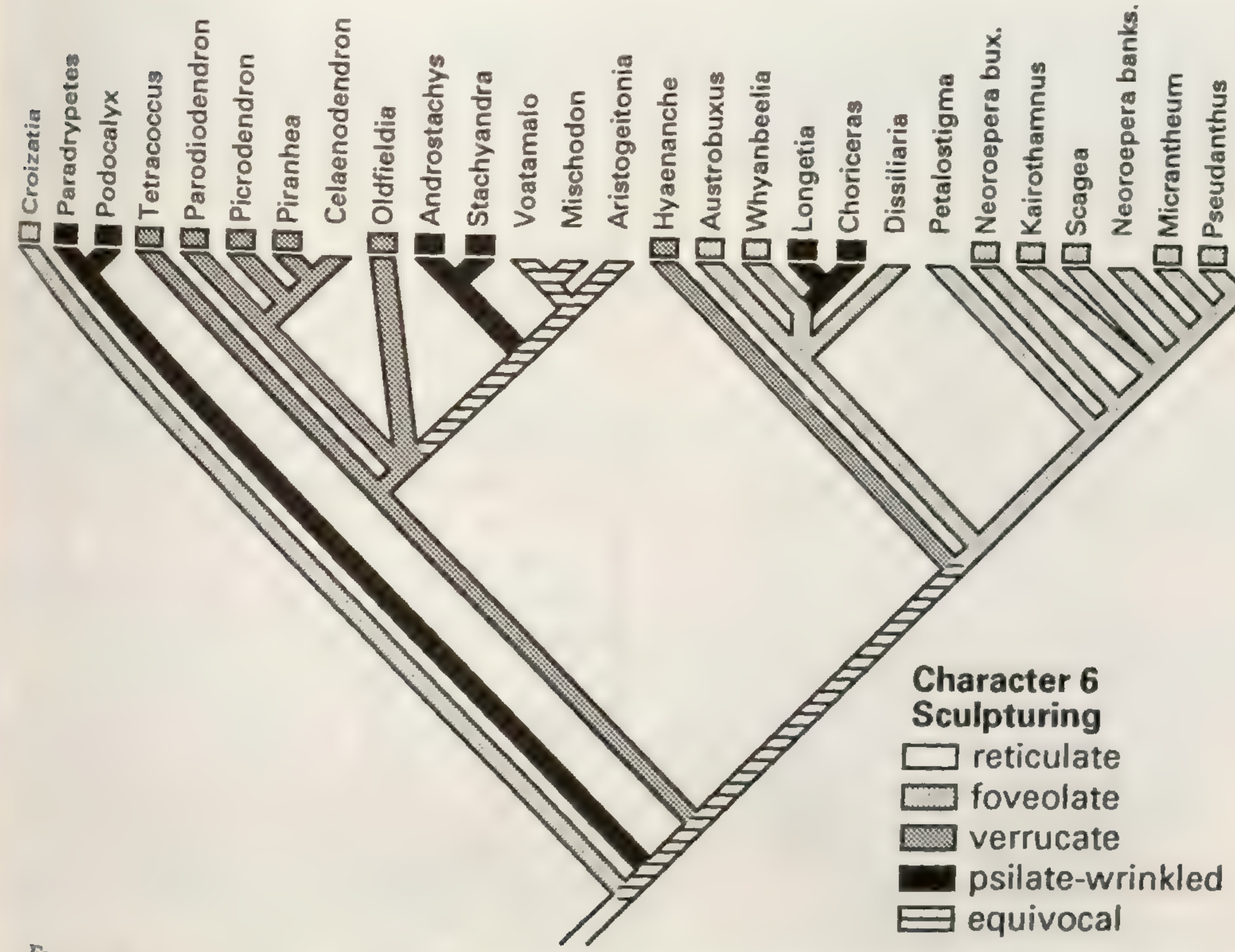


FIGURE 34. Cladogram of the Oldfieldioideae showing character 6, nonspinal sculpturing. Character states found in the taxa are shown by boxes below the taxon names; where there is no box we do not know the state found in that taxon. Note wide distribution of equivocal character states due to homoplasy and unknown states in many taxa.

base requires at least seven additional steps. In contrast, placing *Androstachys* with *Stachyandra* increases the length of the pollen-based tree by only two steps, namely reversals to a thin, homogeneous foot-layer (7: 0) and columellae continuous with the foot-layer (8: 0). The plesiomorphic states for the exine foot-layer and interstitium (characters 7 and 8) found in *Androstachys* are therefore better regarded as reversals rather than as ancestral conditions.

Two characters of reproductive morphology, absence of petals (49: 1) and presence of a caruncle (51: 1), combine with pollen having more than three apertures (2: 1) to support the monophyly of the Oldfieldioideae less *Croizatia*, resulting in the latter genus occupying the basal position in the subfamily (Figs. 30, 31) when our entire data set is considered. Making *Croizatia* the sister group of the clade comprising *Kairothamnus*, *Micrantheum*, *Neoroepera banksii*, *Pseudanthus*, *Scagea*, and *Stachystemon*, as suggested by pollen alone (Fig. 28), increases the length of the combined data set tree by five steps, whereas placing *Croizatia* at the base of the pollen-based tree requires only one additional step. The similarities in exine structure these taxa share, i.e., thick, homogeneous foot-layer (7: 1) and microperforate/granular tectum (9: 3), therefore appear to be convergent between *Croizatia* and the remaining taxa. We must point out that the wood and leaf anatomy of *Croizatia* remains unknown; when studied, such data may support or contradict this hypothesis.

The results of this analysis clarify the synapomorphies of the Oldfieldioideae. As suggested by the tree based on pollen data alone, brevicolporate apertures (4: 1) and echinate pollen (5: 2) are synapomorphies of the subfamily. However, having more than three apertures (2: 1) is not a synapomorphy of the entire subfamily because the basal genus, *Croizatia*, retains the plesiomorphic state of three apertures. The phylogenies illustrated in Figures 31–33 show that having columellae discontinuous from the foot-layer (8: 1) is a further synapomorphy of the subfamily. In addition, though we deleted nonspinal sculpturing (character 6) from our final cladistic analysis and data are missing for several taxa, several patterns can be seen (Fig. 34). Notably, no Oldfieldioideae are known to have reticulate sculpturing (6: 0), the prevalent condi-

TABLE 4. Proposed classification of the Oldfieldioideae. Suprageneric taxa are arranged such that each taxon is the sister group of the taxa of equal rank following it in sequence. "(T)" indicates each type genus.

Tribe I. Croizatieae Webster
  Genus: *Croizatia* Steyerm. (T)
Tribe I. Podocalyceae Webster
  Subtribe Podocalycinae Webster
    Genus: *Podocalyx* Klotzsch (T)
  Subtribe Paradrypetinae G. Levin
    Genus: *Paradrypetes* Kuhlm. (T)
Tribe II. Picrodendreae (Small) Webster
  Subtribe Tetracoccinae G. Levin
    Genus: *Tetracoccus* Engelm. ex C. Parry (T)
  Subtribe Picrodendrinae (Small) Webster
    Genera: *Celaenodendron* Standley, *Parodiodendron* Hunz., *Picrodendron* Planchon (T), *Piranhea* Baillon
  Subtribe Paivaeusinae Pax & K. Hoffmann
    Genus: *Oldfieldia* Benth. & Hook. f. (incl. *Paivaeusa* Welw. ex Benth., T)
  Subtribe Mischodontinae Müll. Arg.
    Genera: *Androstachys* Prain, *Aristogeitonia* Prain (incl. *Parageloniu*m Léandri), *Mischodon* Thwaites (T), *Stachyandra* Radcl.-Sm., *Voatamalo* Capuron ex Bosser
Tribe III. Caletieae Müll. Arg.
  Subtribe Hyaenanchinae Baillon ex Müll. Arg.
    Genus: *Hyaenanche* Lambert (T)
  Subtribe Dissiliariinae Pax & K. Hoffmann
    Genera: *Austrobuxus* Miq. (incl. *Canaca* Guillaumin?), *Choriceras* Baillon, *Dissiliaria* F. Muell. ex Baillon (T), *Longetia* Baillon ex Müll. Arg., *Whyanbeelia* Airy Shaw & B. Hyland
  Subtribe Petalostigmatinae Pax & K. Hoffmann
    Genus: *Petalostigma* F. Muell. (T)
  Subtribe Pseudanthinae Müll. Arg.
    Genera: *Kairothamnus* Airy Shaw, *Micrantheum* Desf., *Neoroepera* Müll. Arg., *Pseudanthus* Sieber ex Sprengel (T), *Scagea* McPherson, *Stachystemon* Planchon

tion in the Phyllanthoideae. Therefore nonreticulate sculpturing may be said to characterize the Oldfieldioideae.

Further aspects of pollen character evolution are discussed by Simpson & Levin (in press), and evolutionary patterns of most of the vegetative characters have been discussed by Hayden (1994). Here we will concentrate on the taxonomic implications of the synapomorphies shown in Figures 31–33.

TAXONOMIC IMPLICATIONS

Since Köhler (1965) first recognized the Oldfieldioideae as a distinct subfamily and subdivided it into tribes, three further treatments of the subfamily have been proposed. Hutchinson (1969) did not recognize any subfamilies, and his treatment can be essentially ignored because he disregarded the palynological data compiled by Punt (1962) and Köhler (1965) and scattered the oldfieldioid genera among five tribes, three of them also containing phyllanthoid genera. He was the first, however, to place *Paradrypetes* with other genera of the Oldfieldioideae. Webster (1975, 1994), in contrast, relied heavily on palynology and presented major reorganizations of the subfamily. With the exception of Webster's (1994) recent classification, none of these treatments agrees very well with either of the preferred phylogenies based on our combined data set (Figs. 31–33).

Though we are somewhat reluctant to propose a formal classification of the Oldfieldioideae given the paucity of reproductive morphological data in our analysis, we find it useful to summarize our findings in the form of a system. We therefore propose the classification shown in Table 4 and Figure 35, in which all the suprageneric taxa are monophyletic according to our preferred phylogenies (Figs. 31–33). We have not given coordinate taxa equal rank, but for suprageneric taxa have followed the sequencing convention proposed by Wiley (1979, 1981: 205–225), wherein each taxon is the sister group of the taxon or taxa of equal rank following it in sequence. Within suprageneric taxa we list genera alphabetically. Our classification is almost identical to that of Webster (1994), differing only in the placement of *Tetracoccus* (see below).

We divide the Oldfieldioideae into four tribes. The first tribe, the Croizatieae, consists solely of the genus *Croizatia*. The remaining Oldfieldioideae share two unique synapomorphies (Fig. 31): pollen with more than three apertures (2: 1) and petals absent (49: 1). Two homoplastic synapomorphies also characterize the rest of the Oldfieldioideae: exinous foot-layer reduced or absent (7: 2; Fig. 36), which shows further evolution and convergence elsewhere in the tree, and caruncles present on the seeds (51: 1), which shows repeated losses in isolated genera. It is tempting to view opposite or whorled leaves (25: 1; Fig. 37) as a synapomorphy of the Oldfieldioideae above *Croizatia*, because opposite or whorled leaves (25: 1) are common in the Oldfieldioideae and leaves of the Phyllanthoideae are consistently alternate, as are leaves of the primitive members of the other subfamilies. In fact, this character varies in such a way that it is impossible, using parsimony alone, to determine the state at most levels within the

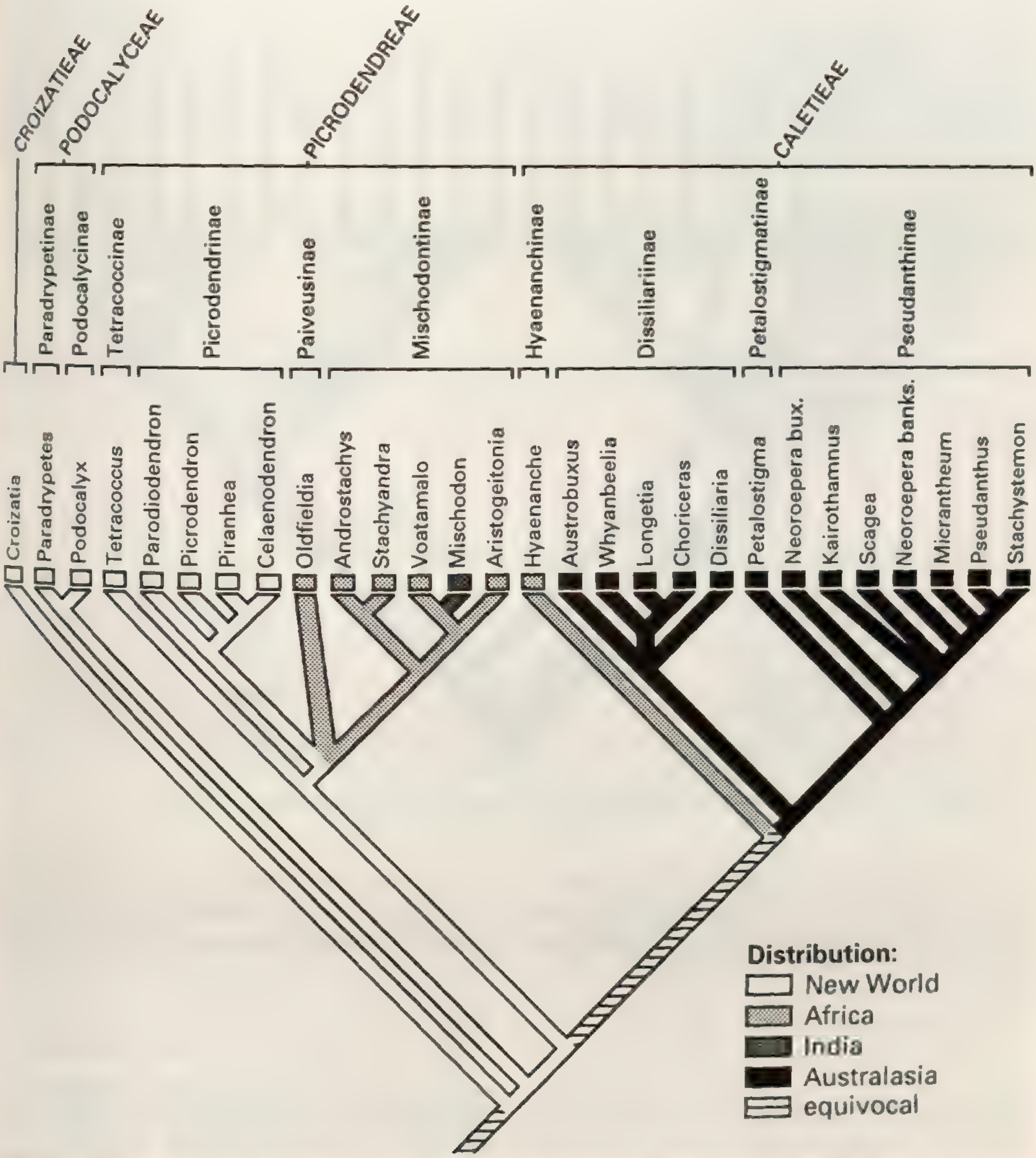


FIGURE 35. Cladogram of Oldfieldioideae showing the geographic distribution of the taxa and our proposed classification of the Oldfieldioideae.

subfamily (Fig. 37). In *Picrodendron*, the first pair of leaves above the cotyledons are opposite, though the remaining leaves are alternate (Hayden et al., 1984). Examination of the other alternate-leaved Oldfieldioideae could clarify whether this is developmental evidence that could aid in the determination of the polarity of this character.

Given the number of synapomorphies shared by most of the Oldfieldioideae but lacking in *Croizatia* (Fig. 31), it could argued that this genus should be retained in the Phyllanthoideae. Our data, however, leave little doubt that *Croizatia* is the sister group of the remaining Oldfieldioideae. Furthermore, the position of *Croizatia* is ambiguous if it is retained in the Phyllanthoideae (Webster et al., 1987). We therefore find it more informative to treat *Croizatia* as the basal member of the Oldfieldioideae.

The second tribe, the Podocalyceae, is supported by a single unique synapomorphy, reduction or loss of the interstitial elements in the exine (8: 2). In addition, unsclerified crystalliferous axial xylem parenchyma (21: 1), convergent elsewhere in the tree, supports this clade (Fig. 31). Psilate-wrinkled

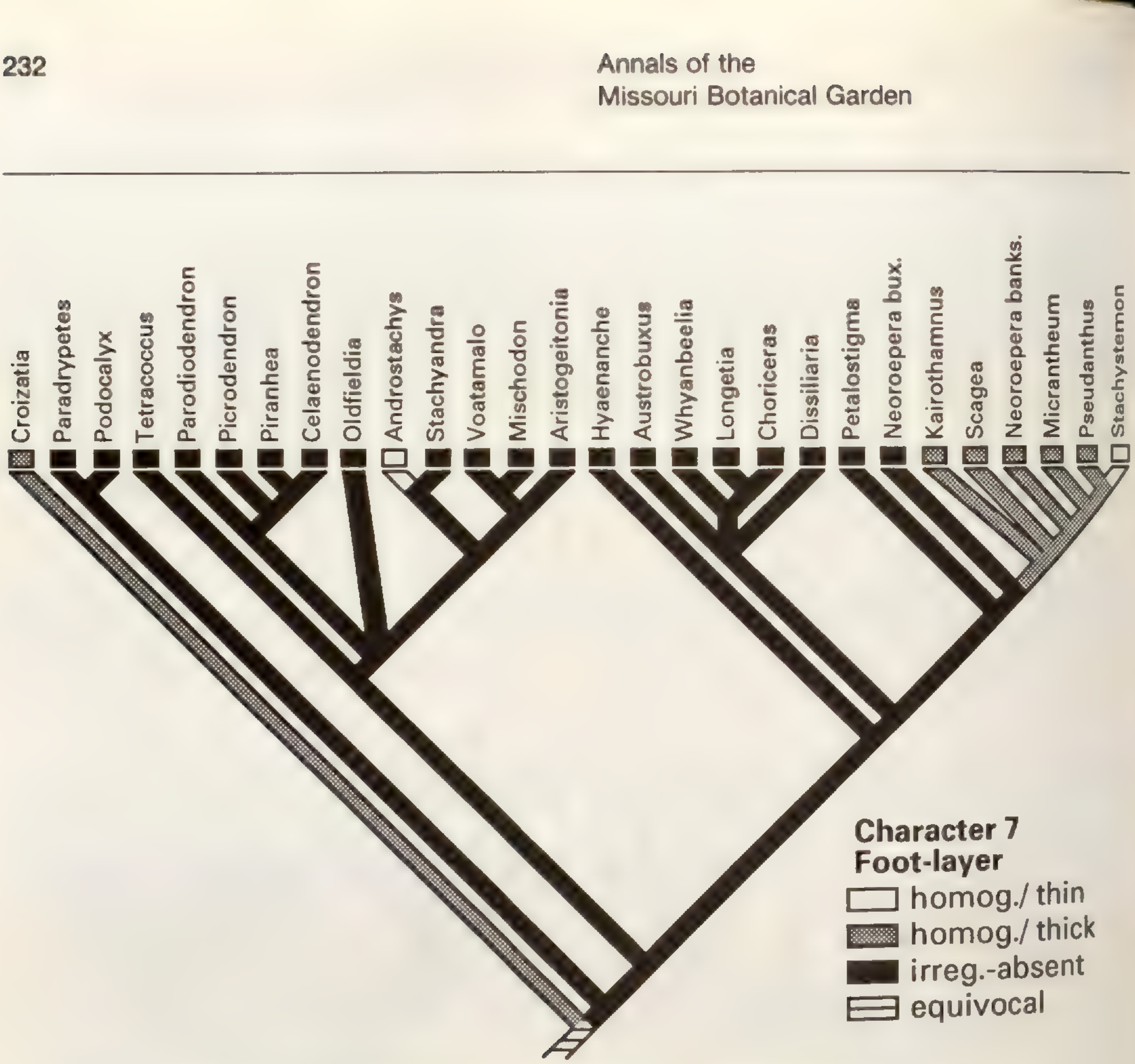


FIGURE 36. Cladogram of Oldfieldioideae showing character 7, pollen ektexinous foot-layer.

nonspinal sculpturing (6: 4) may also be a synapomorphy of this clade, but unfortunately the ancestral state for this character in the Oldfieldioideae is ambiguous (Fig. 34). Because *Paradrypetes* and *Podocalyx* are so different from each other (Levin, 1992), we place each in its own subtribe.

The rest of the Oldfieldioideae share two unique synapomorphies (Fig. 31), simple perforation plates (12: 1) and alternate intervascular pitting (13: 1), and one, microperforate/baculate tectum (9: 2; Fig. 38), that evolves to other derived states higher within the clade. It is tempting to interpret verrucate nonspinal sculpturing (6: 3) as a synapomorphy of this clade, but the ancestral state is equivocal (Fig. 34). We divide this clade into two tribes representing a major split within the subfamily.

The first of these tribes, the Picrodendreae (Fig. 32), is defined by having alternate vessel-ray pitting (18: 1), a synapomorphy that is convergent elsewhere. *Tetracoccus*, the basal member of this clade, has several autapomorphies and we therefore propose placing it in its own subtribe, the Tetracoccinae (G. Levin in Webster, 1994). Webster placed the Tetracoccinae in the Podocalyceae, emphasizing that the pollen of *Tetracoccus*, like that of both *Paradrypetes* and *Podocalyx*, has four brevicolporate apertures. This state appears to be plesiomorphic at this level in the tree, and treating *Tetracoccus* plus the Podocalyceae as a monophyletic group lengthens the combined data trees (Figs. 31–33) by three steps.

The rest of the Picrodendreae share four homoplastic synapomorphies (Fig. 32): compound or unifoliolate leaves (24: 1, 2), bundle sheath extensions (33: 1), fimbriate marginal venation (39: 1), and well-developed areoles (42: 1). We recognize three subtribes in the Picrodendreae, representing the three clades of this trichotomy. *Oldfieldia*, the sole genus of Paivaeusinae, has no synapomorphies that clearly unite it with either clade. Indeed, our data provide no support for the monophyly of *Oldfieldia*, which has four species; given the variation in phyllotaxy within the genus (Fig. 37), the possibility that it is not monophyletic should be examined. Genera in the American subtribe Picrodendrinae (Fig. 32) share one unique synapomorphy, loss of crystals in the mesophyll (32: 1), and two homoplastic synapomorphies, larger than typical intervascular pitting (14: 1) and prismatic crystals in the bundle sheath extensions (34: 1). Leaves are uniformly alternate (25: 0) in the Picroden-

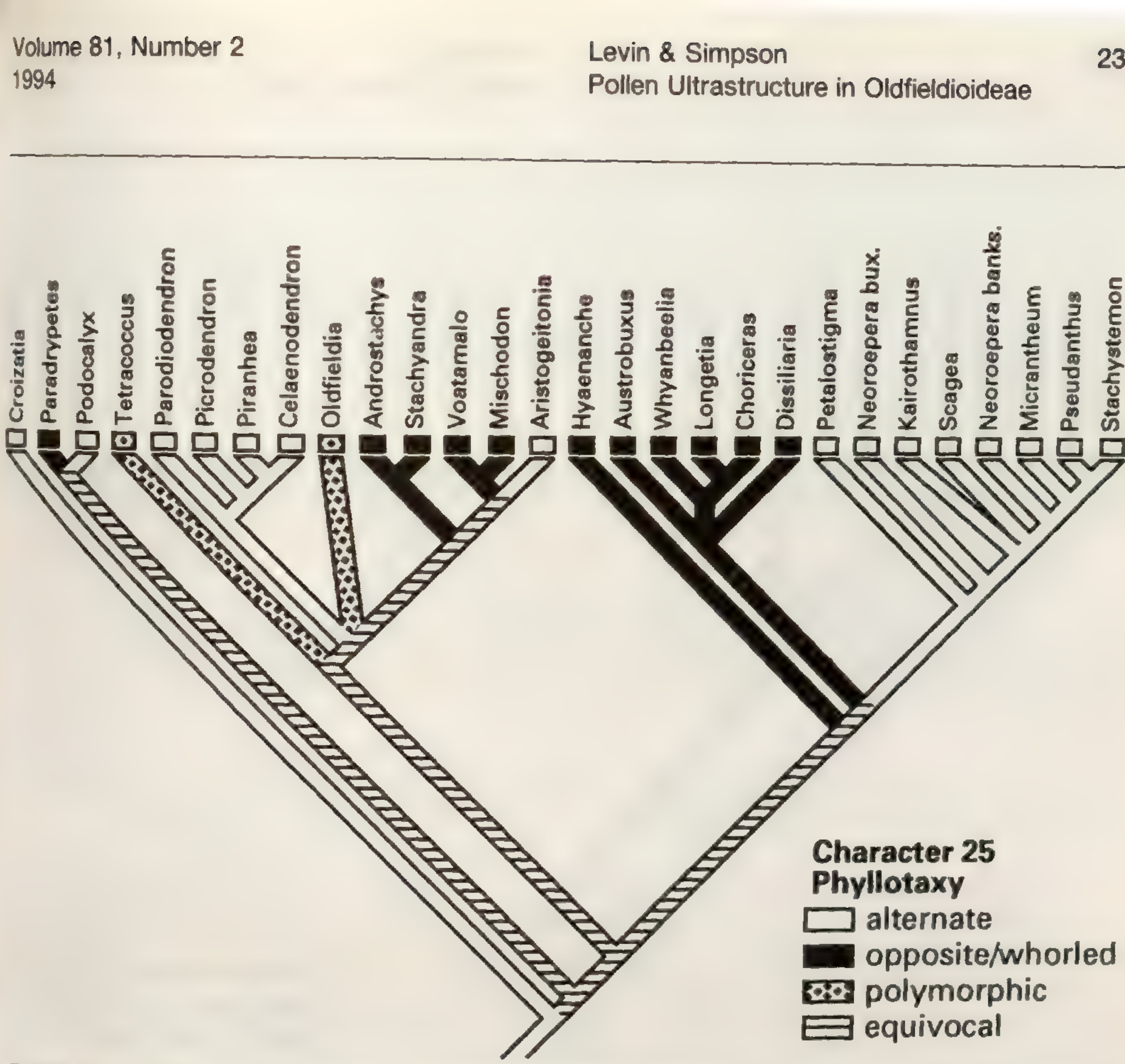


FIGURE 37. Cladogram of Oldfieldioideae showing character 25, phyllotaxy. Note that the polarity of this character within the Oldfieldioideae cannot be determined in most of the tree.

drinae, but whether this is a synapomorphy or a symplesiomorphy is equivocal (Fig. 37). Further homoplastic synapomorphies resolve relationships among the four genera in this subtribe (Fig. 32). The final subtribe we recognize in the Picrodendreae, the African/Indian Mischodontinae, shares the unique synapomorphy epipetiolar stipules (46: 1). *Androstachys* and *Stachyandra* form the basal clade, defined by one unique synapomorphy, columnar foliar sclereids (44: 1), and two homoplastic synapomorphies, homogeneous tectum (9: 1; Fig. 38) and vein order beyond the tertiaries indistinguishable (41: 1). The remaining genera share the homoplastic synapomorphy of sclerified crystalliferous ray cells (19: 1). As we noted above in the discussion of this character, interpretation of this character in the Phyllanthoideae and the outgroups is somewhat doubtful. However, this clade is also supported by the homoplastic synapomorphy of epidermal mucilage lacking (26: 1). Reversal to simple leaves (24: 0) unites *Mischodon* and *Voatamalo* (Fig. 32).

The final tribe, Caletieae (Fig. 33), is defined by the unique synapomorphy of crenulate anticlinal walls on the subsidiary cells (30: 1, Fig. 31). The South African genus *Hyaenanche*, the basal member of the clade, also is the sole member found outside Australasia (Fig. 35). We propose maintaining it in its own subtribe, recognizing its unique distribution and gross morphology. We are unable to choose between two slightly different phylogenies for the remaining genera in the tribe (Fig. 33) because our data support both equally well. All these genera share chambered epidermal cells (27: 1), a unique synapomorphy, and depending on the phylogeny chosen, the clade may also be defined by sclerified crystalliferous axial xylem parenchyma (21: 1). These genera also share nonverrucate sculpturing, either foveolate (6: 1) or psilate-wrinkled (6: 4), but whether either of these states can be considered a synapomorphy at this level is equivocal (Fig. 34). In either case, we recognize three additional subtribes within the Caletieae.

Reduced or obsolete stipules (45: 1), a unique synapomorphy, and ektexinous periapertural thickenings (10: 1), convergent in *Croizatia*, unite the genera we assign to the subtribe Dissiliariinae (Fig. 33). Though our data for these two characters are incomplete for these taxa (see Table 3 and the discussion above of character 45), for each genus

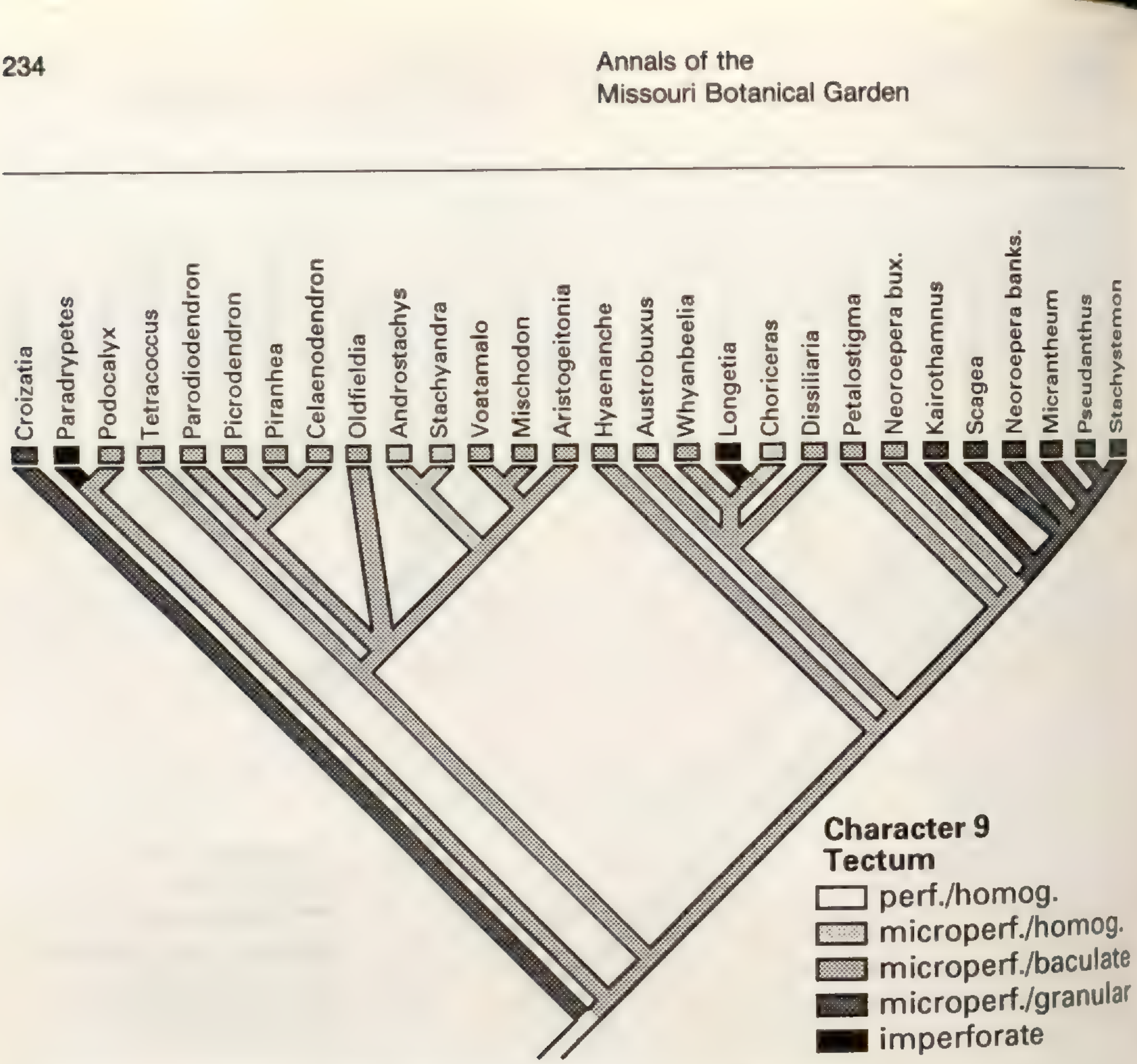


FIGURE 38. Cladogram of Oldfieldioideae showing character 9, the tectum.

we have definite data for at least one of the characters. In combination, therefore, these two characters provide unequivocal support for this clade. Within the Dissiliariinae, sexuality (character 48) distinguishes *Austrobuxus* and *Dissiliaria* from *Choriceras*, *Longetia*, and *Whyanbeelia* (Fig. 33). Though authors, including Airy Shaw (1974, 1976, 1980) and McPherson (1985), have used sexuality as a means of segregating taxa from *Austrobuxus*, this is the first demonstration of the phylogenetic significance of this character in the Oldfieldioideae. Unfortunately, the polarity of this character at this level in the tree depends on the phylogeny chosen (Fig. 33). *Choriceras* and *Longetia* are united by minute pollen spines (5: 1), a unique synapomorphy. As noted above, the microperforate/homogeneous tectum (9: 1) of *Choriceras* can be interpreted as transitional between the microperforate/baculate tectum (9: 2) of most other Oldfieldioideae and the imperforate tectum (9: 4) of *Longetia*, further supporting a close relationship. Our data clearly support the separation of *Longetia* from *Austrobuxus* as advocated by McPherson & Tirel (1987).

In recognition of its distinctive autapomorphies and its doubtful placement (Fig. 33), we maintain *Petalostigma* in its own subtribe, the Petalostigmatinae. Whether this subtribe or the Dissiliariinae is more closely related to the final subtribe, the Pseudanthinae, is ambiguous (Fig. 33). As we discussed previously, some species of *Petalostigma* have pollen in which the apertures do not all lie on the equator. If this is transitional to the pantoporate condition in the Pseudanthinae, it would suggest that *Petalostigma* is more closely related to the Pseudanthinae. In either case, the thin-walled unlignified phloem fibers in the primary leaf vein of *Petalostigma* (31: 2) appear to have evolved independently from the thick-walled unlignified phloem fibers of many of the Pseudanthinae (31: 1), demonstrating the lack of homology between loss of lignification in these two types of fibers.

The core genera of the Pseudanthinae, *Micrantheum*, *Pseudanthus*, and *Stachystemon*, were first placed together in 1858 (Ågardh, 1858) and have remained so in virtually every system since then. Punt (1962) and Köhler (1965) recognized that *Neoroepera* is closely related to these genera—all share pantoporate pollen (3: 1)—and Webster (1975) added the genus to the subtribe. Now we can add *Kairothamnus* and *Scagea*, as their pollen, too, is pantoporate. These results also

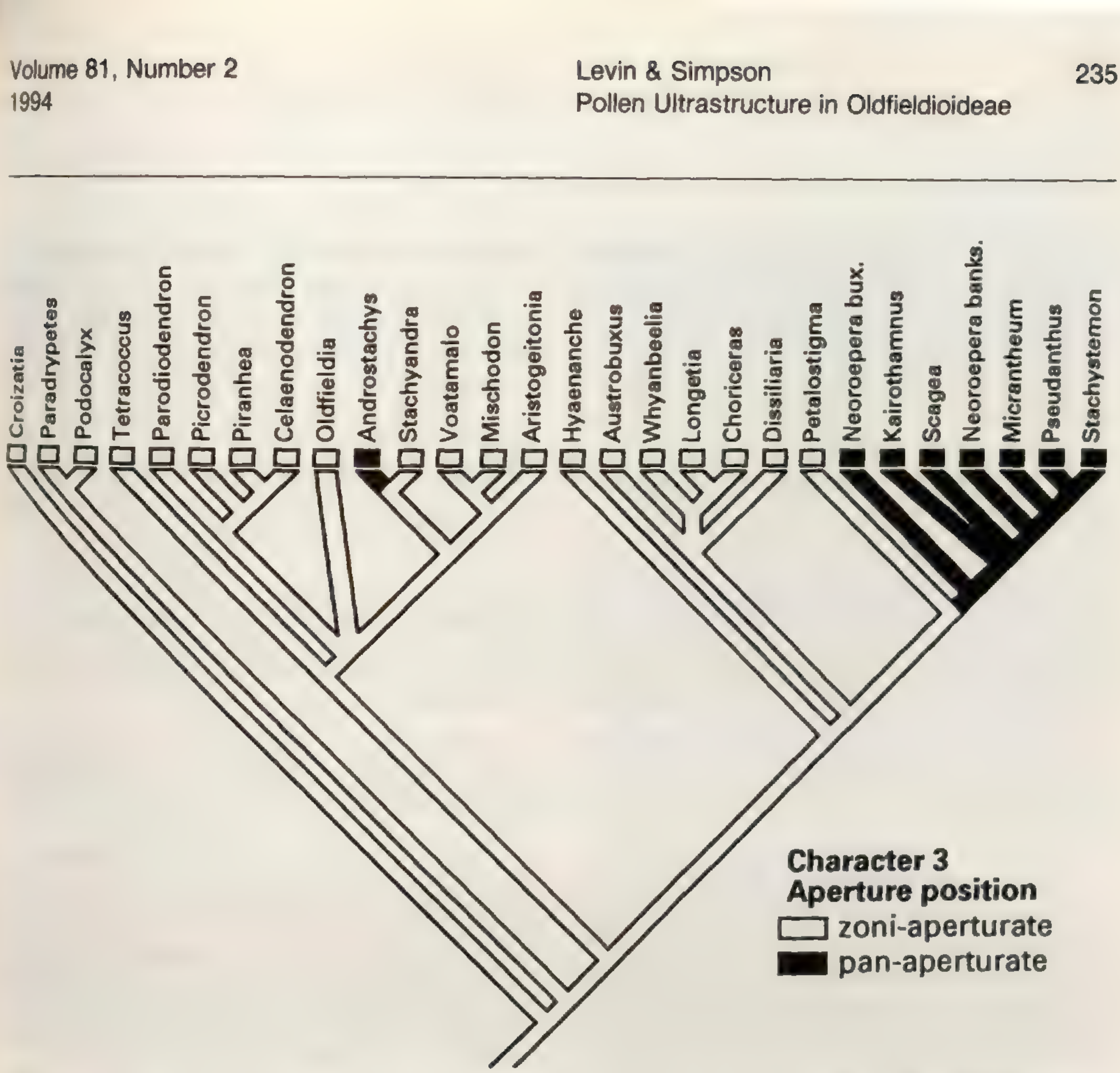


FIGURE 39. Cladogram of Oldfieldioideae showing character 3, pollen aperture position. Pan-aperturate pollen has evolved twice, once in *Androstachys* and once in the Pseudanthinae.

reinforce our earlier conclusion that pantoporate apertures evolved independently in *Androstachys* and in the Pseudanthinae (Fig. 39). The woods of *Kairothamnus* and *Scagea* have not been examined, but it appears that two wood synapomorphies, homocellular erect rays (16: 1; unique) and alternate vessel-ray pitting (18: 1; homoplastic), also unite the Pseudanthinae (Fig. 33). All the genera in the subtribe are monoecious (48: 1), but whether this is a synapomorphy of this subtribe or of a larger group is ambiguous (Fig. 33).

Though McPherson & Tirel (1987) discovered that *Scagea* is pantoporate, they were impressed by its uniovulate carpels and placed it in the Crotonoideae. Our studies show that *Scagea* instead belongs in the Pseudanthinae. Pollen ultrastructure of Crotonoideae, though variable, is quite different from that of *Scagea* (Nowicke, 1994, this issue). As we discussed previously in the section on cladistic analysis of the palynological data, *Scagea* instead shares the unique ultrastructural synapomorphies of the other Pseudanthinae (except *Neoroepera buxifolia*; see Fig. 33), notably a thick, homogeneous foot-layer (7: 1; Fig. 36) and a microperforate/granular tectum (9: 3; Fig. 38). So far as is known (its wood has not been examined), *Scagea* also shares the morphological synapomorphies expected of a genus nested within the Pseudanthinae, making it unlikely that *Scagea* belongs elsewhere. Specifically, it has chambered epidermal cells (27: 1; Fig. 33) and crenulate anticlinal walls on the subsidiary cells (30: 1; Fig. 31), both unique synapomorphies within the Oldfieldioideae; crenulate subsidiary cells are not known elsewhere in the Euphorbiaceae (Hayden, 1994). Also unique in Oldfieldioideae is having the cotyledons narrower than the radicle (23: 1), a synapomorphy shared by *Micrantheum*, *Pseudanthus*, and *Stachystemon* (Fig. 33); seeds of *Scagea* (and *Kairothamnus*) should be examined to determine the form of its embryo. Like the other Pseudanthinae, *Scagea* is monoecious.

On the basis of our data *Neoroepera* appears to be diphyletic, in that *N. banksii* shares with other Pseudanthinae four synapomorphies that are lacking in *N. buxifolia*. With *Kairothamnus*, *Scagea*, *Micrantheum*, *Pseudanthus*, and *Stachystemon*, *N. banksii* shares a thick, homogeneous foot-layer (7: 1; Fig. 36) and a microperforate/granular tectum (9: 3; Fig. 38), both unique within the

Oldfieldioideae, and with the last three genera shares thick unlignified phloem fibers in the primary leaf vein (31: 1) and an intramarginal leaf vein (38: 1), both also unique synapomorphies (Fig. 33). *Neoroepera buxifolia* is the type species, so it appears that a new genus will have to be described to accommodate *N. banksii* (Levin, in prep.).

As we discussed previously when explaining character state coding, it is unclear whether *Micrantheum* bears sessile compound exstipulate leaves or simple leaves with foliaceous stipules. This cladistic analysis shows that within the Oldfieldioideae compound leaves (24: 1, 2) are restricted to the Picrodendreae and loss of stipules (45: 1) to the Dissiliariinae. It is therefore more parsimonious to interpret the leaves of *Micrantheum* as being simple with foliaceous stipules.

BIOGEOGRAPHY

The phylogenies shown in Figures 31–33 fit very well with the distribution of the genera (Fig. 35). *Croizatia*, *Paradrypetes*, and *Podocalyx*, which form the basal two clades, are all American, as are *Tetracoccus* and the four genera we place in the Picrodendrinae, *Celaenodendron*, *Parodiodendron*, *Picrodendron*, and *Piranhea*. In contrast, *Oldfieldia* and the Mischodontinae are African and/or Madagascan, with the exception of *Mischodon* itself which is found in India and Sri Lanka. With the sole exception of the South African endemic *Hyaenanche*, the remaining genera are all Australasian.

RELATIONSHIPS WITH OTHER EUPHORBIACEAE

It is clear that Oldfieldioideae are derived from within the Phyllanthoideae (Hayden, 1994; Webster, 1994; Webster et al., 1987). We have not studied the pollen ultrastructure of enough Phyllanthoideae, particularly the relatively basal genera, to be able to use those data to resolve relationships further. Uncertainty about appropriate outgroups also limited resolution of relationships among the Phyllanthoideae we did study and between these taxa and the Oldfieldioideae. At this point we can do little more than speculate that the closest relatives of the Oldfieldioideae are probably among the relatively basal Phyllanthoideae.

As pointed out by Webster et al. (1987), the resemblance between pollen of *Amanoa guianensis* and Oldfieldioideae is superficial. Though the pollen of *A. guianensis* may appear to be echinate with verrucate nonspinal sculpturing (Webster et al., 1987: fig. 7), the pollen has a thin, continuous foot-layer (7: 0) like other Phyllanthoideae. Furthermore, pollen of *A. guianensis* is intectate: the verrucae and round-ended spines—or baculae—originate from the foot-layer rather than the tectum (Fig. 14). Thus the pollen of *A. guianensis* does not support a close relationship between this species and the Oldfieldioideae. Instead, *A. guianensis* appears to be a derived species within a genus that otherwise has tectate-reticulate pollen (Simpson & Levin, in prep.; Köhler, 1965; Punt, 1962), as seen, for example, in *A. strobilacea* (Fig. 15).

RECOMMENDATIONS FOR FUTURE RESEARCH

This study confirms that pollen studies using TEM, like those using LM and SEM, can contribute data of systematic significance for the Euphorbiaceae. Nowicke's (1994) study of Crotonoideae provides additional evidence for the utility of TEM data. Given our ignorance of pollen ultrastructure throughout most of the family, we recommend starting with general surveys of the remaining three subfamilies, paying particular attention to relatively basal genera in the various lineages.

By combining our pollen data with the excellent data on the vegetative morphology and anatomy obtained by Hayden (1980, 1994), we have been able to propose a strong hypothesis for the phylogeny of the Oldfieldioideae. Unfortunately we have largely neglected reproductive morphology in our analysis. This is due in large part to inconsistent descriptions and lack of published data. There is a pressing need for a careful comprehensive review of reproductive morphology throughout the Oldfieldioideae. When those data are available, systematists can further test and refine the phylogeny and classification we have proposed.

Certain taxa also require further study of their vegetative anatomy because these data currently are unavailable (see Table 3). Critical among these taxa is *Croizatia* because of its apparently basal position within the subfamily; both its wood and foliar anatomy are poorly known. Other taxa requiring further study are *Kairothamnus*, *Longetia*, *Scagea*, and *Stachystemon*, for all of which we lack data on wood anatomy, and *Voatamalo*, for which we lack data on foliar morphology and anatomy.

Chromosome numbers are known for only two species in the Oldfieldioideae, *Mischodon zeylanicus* and *Tetracoccus fasciculatus* (S. Watson) Croizat. Both have $x = 12$ (Datta, 1967; Perry, 1943; Sarkar & Datta, 1980), whereas the base number for most Phyllanthoideae is $x = 13$ (Hans, 1973). Chromosome counts for more Oldfieldioideae are needed to determine if chromosome num-

ber provides an additional synapomorphy for the subfamily, further clarifying its limits.

Literature Cited

Agardh, C. A. 1858. Theoria Systematis Plantarum. Gleerup, Lund.

Airy Shaw, H. K. 1970. The genus *Androstachys* Prain in Madagascar. Adansonia, sér. 2, 10: 519–524.

———. 1972. A second species of the genus *Aristogeitonia* Prain (Euphorbiaceae) from East Africa. Kew Bull. 26: 495–498.

———. 1974. Notes on Malesian and other Asiatic Euphorbiaceae. CLXXV. New species of *Austrobuxus* Miq., with a key to the whole genus. Kew Bull. 29: 303–309.

———. 1976. New or noteworthy Australian Euphorbiaceae. Kew Bull. 31: 341–398.

———. 1980. New Euphorbiaceae from New Guinea. Kew Bull. 34: 591–598.

Bonnefille, R. & G. Riollet. 1980. Pollens des Savanes d'Afrique Oriental. Centre National de la Recherche Scientifique, Paris.

Bosser, J. 1976. *Voatamalo*, nouveau genre d'*Euphorbiaceae* de Madagascar. Adansonia, sér. 2, 15: 333–340.

Chase, M. W., W. R. Anderson & H. G. Hills. 1991. Molecular systematics of the Malpighiaceae and "middle rosid" families: An analysis of variation in gene sequences from the chloroplast gene *rbc*L. Amer. J. Bot. 78(6, supplement): 170.

Cronquist, A. 1981. The Evolution and Classification of Flowering Plants. Houghton Mifflin, Boston, Massachusetts.

Dahlgren, R. 1983. General aspects of angiosperm evolution and macrosystematics. Nordic J. Bot. 3: 119–149.

——— & A. E. van Wyk. 1988. Structures and relationships of families endemic to or centered in southern Africa. Monogr. Syst. Bot. Missouri Bot. Gard. 25: 1–94.

Datta, N. 1967. *In:* A. Löve (editor), IOPB Chromosome Number Reports XII. Taxon 16: 341–350.

Dechamps, R., M. Mosango & E. Robbrecht. 1985. Etudes systématiques sur les Hymenocardiaceae d'Afrique: La morphologie du pollen et l'anatomie du bois. Bull. Jard. Bot. Etat 55: 473–485.

Donoghue, M. J. & P. D. Cantino. 1984. The logic and limitations of the outgroup substitution approach to cladistic analysis. Syst. Bot. 9: 192–202.

El-Ghazaly, G. & B. Raj. 1986. A contribution to the pollen morphology of *Andrachne* (Euphorbiaceae). Pollen & Spores 28: 297–310.

Erdtman, G. 1952. Pollen Morphology and Plant Taxonomy, Angiosperms. Almqvist & Wiksell, Stockholm.

Farris, J. S. 1969. A successive approximations approach to character weighting. Syst. Zool. 18: 374–385.

———. 1988. Hennig86, ver. 1.5. Computer program distributed by James S. Farris, Port Jefferson Station, New York.

Hans, A. S. 1973. Chromosomal conspectus of the Euphorbiaceae. Taxon 22: 591–636.

Hayden, W. J. 1977. Comparative anatomy and systematics of *Picrodendron, genus incertae sedis*. J. Arnold Arbor. 58: 257–279.

———. 1980. Systematic anatomy of Oldfieldioideae (Euphorbiaceae). Unpublished Ph.D. Dissertation. Univ. Maryland, College Park.

———. 1994. Systematic anatomy of Euphorbiaceae subfamily Oldfieldioideae. I. Overview. Ann. Missouri Bot. Gard. 81: 000–000.

———, W. T. Gillis, D. E. Stone, C. R. Broome & G. L. Webster. 1984. Systematics and palynology of *Picrodendron*: Further evidence for relationship with the Oldfieldioideae (Euphorbiaceae). J. Arnold Arbor. 65: 105–127.

Herr, J. M., Jr. 1971. A new clearing-squash technique for the study of ovule development in angiosperms. Amer. J. Bot. 58: 785–790.

Hickey, L. J. 1979. A revised classification of the architecture of dicotyledonous leaves. Pp. 25–39 *in* C. R. Metcalfe & L. Chalk (editors), Anatomy of the Dicotyledons, 2nd ed., Vol. 1. Clarendon Press, Oxford.

——— & J. A. Wolfe. 1975. The bases of angiosperm phylogeny: Vegetative morphology. Ann. Missouri Bot. Gard. 62: 538–589.

Hutchinson, J. 1969. Tribalism in the family Euphorbiaceae. Amer. J. Bot. 56: 738–758.

Jussieu, A. H. L. de. 1824. De Euphorbiacearum Generibus Medicisque Earumdem Viribus Tentamen. Didot, Paris.

Köhler, E. 1965. Die Pollenmorphologie der Biovulaten Euphorbiaceae und ihre Bedeutung für die Taxonomie. Grana Palynol. 6: 26–120.

Kuhlmann, J. G. 1935. Novas especies da Hylea. Arq. Inst. Biol. Veg. 2: 83–89.

———. 1940. Especies novas equatoriais. Anais Reunião Sul.-Amer. Bot. 3: 78–86.

Leroy, J.-F. 1976. Recherches sur la nature et l'origine de la fleur angiospermienne: Interprétation des structures dans un groupe singulier d'Euphorbiaceae. Compt. Rend. Hebd. Séances Acad. Sci., Sér. D, 283: 147–150.

Levin, G. A. 1986a. Systematic foliar morphology of Phyllanthoideae (Euphorbiaceae). I. Conspectus. Ann. Missouri Bot. Gard. 73: 29–85.

———. 1986b. Systematic foliar morphology of Phyllanthoideae (Euphorbiaceae). II. Phenetic analysis. Ann. Missouri Bot. Gard. 73: 86–98.

———. 1986c. Systematic foliar morphology of Phyllanthoideae (Euphorbiaceae). III. Cladistic analysis. Syst. Bot. 11: 515–530.

———. 1992. Systematics of *Paradrypetes* (Euphorbiaceae). Syst. Bot. 17: 74–83.

——— & M. G. Simpson. 1994. Phylogenetic relationships of *Didymocistus* and *Hymenocardia* (Euphorbiaceae). Ann. Missouri Bot. Gard. 81: 239–244.

Maddison, W. P. & D. R. Maddison. 1992. MacClade: Analysis of Phylogeny and Character Evolution, ver. 3.0. Sinauer Associates, Sunderland, Massachusetts.

———, M. J. Donoghue & D. R. Maddison. 1984. Outgroup analysis and parsimony. Syst. Zool. 33: 83–103.

Martin, H. A. 1974. The identification of some Tertiary pollen belonging to the family Euphorbiaceae. Austral. J. Bot. 22: 271–291.

Matos Araujo, P. A. de & A. de Mattos Filho. 1984. Estrutura das madeiras brasileiras de Dicotiledô-

neas—XXVI. Euphorbiaceae. Rodriguésia 36: 25–40.

McPherson, G. 1985. *Scagea*, a new genus of Euphorbiaceae from New Caledonia. Bull. Mus. Hist. Nat. (Paris), sér. 4, sect. B, Adansonia 7: 247–250.

——— & G. Tirel. 1987. Euphorbiaceae. I. Euphorbioideae, Crotonoideae, Acalyphoideae, Oldfieldioideae. *In:* P. Morat & H. S. Mackee (editors), Flore de la Nouvelle-Calédonie et Dépendances 14: 1–226. Muséum National d'Histoire Naturelle, Paris.

Mennega, A. M. W. 1984. Wood structure of *Jablonskia congesta* (Euphorbiaceae). Syst. Bot. 9: 236–239.

———. 1987. Wood anatomy of the Euphorbiaceae, in particular of the subfamily Phyllanthoideae. J. Linn. Soc., Bot. 94: 111–126.

Metcalfe, C. R. & L. Chalk. 1950. Anatomy of the Dicotyledons, 1st ed., Vol. 2. Oxford Univ. Press, Oxford.

Milanez, F. R. 1935. Anatomia de *Paradrypetes ilicifolia*. Arq. Inst. Biol. Veg. 2: 133–156.

Nowicke, J. 1994. A palynological study of Crotonoideae (Euphorbiaceae). Ann. Missouri Bot. Gard. 81: 245–269.

Pax, F. & K. Hoffmann. 1922. Euphorbiaceae–Phyllanthoideae–Phyllantheae. *In:* A. Engler (editor), Das Pflanzenreich, IV, 147. XV (Heft 81): 1–349.

——— & ———. 1931. Euphorbiaceae. *In:* A. Engler & K. Prantl (editors), Die Natürlichen Pflanzenfamilien, ed. 2, 19c: 11–233.

Perry, B. A. 1943. Chromosome number and phylogenetic relationships in the Euphorbiaceae. Amer. J. Bot. 30: 527–543.

Poole, M. M. 1981. Pollen diversity in *Zimmermannia* (Euphorbiaceae). Kew Bull. 36: 129–138.

Punt, W. 1962. Pollen morphology of the Euphorbiaceae with special reference to taxonomy. Wentia 7: 1–116.

———. 1980. Pollen morphology of the *Phyllanthus* species (Euphorbiaceae) occurring in New Guinea. Rev. Palaeobot. Palynol. 31: 155–177.

———. 1987. A survey of pollen morphology in Euphorbiaceae with special reference to *Phyllanthus*. J. Linn. Soc., Bot. 94: 127–142.

Radcliffe-Smith, A. 1987a. Euphorbiaceae (Part 1). *In:* R. M. Polhill (editor), Flora of Tropical East Africa. A. A. Balkema, Rotterdam.

———. 1987b. Notes on Madagascan Euphorbiaceae. I. On the identity of *Paragelonium* and on the affinities of *Benoistia* and *Claoxylopsis* (Euphorbiaceae). Kew Bull. 43: 625–647.

———. 1990. Notes on Madagascan Euphorbiaceae. III. *Stachyandra*. Kew Bull. 45: 561–568.

Radford, A. E., W. C. Dickison, J. R. Massey & C. R. Bell. 1974. Vascular Plant Systematics. Harper & Row, New York.

Reitsma, T. 1970. Suggestions towards unification of descriptive terminology of angiosperm pollen grains. Rev. Palaeobiol. Palynol. 10: 39–60.

Sarkar, A. K. & N. Datta. 1980. Cytological assessment of the family Euphorbiaceae. II. Tribe Phyllantheae. Proc. Indian Sci. Congr. Assoc. (III, C) 67: 48–49.

Simpson, M. G. & G. A. Levin. Pollen ultrastructure of the biovulate Euphorbiaceae. Int. J. Pl. Sci. (in press).

Spurr, A. 1969. A low-viscosity epoxy resin embedding medium for electron microscopy. J. Ultrastruct. Res. 26: 31–43.

Standley, P. C. 1927. *Celaenodendron*. Pp. 76–77 *in* R. S. Ferris (editor), Preliminary Report on the Flora of the Tres Marías Islands. Contr. Dudley Herb. 1: 63–88.

Stevens, P. F. 1991. Character states, morphological variation, and phylogenetic analysis: A review. Syst. Bot. 16: 553–583.

Swofford, D. L. 1993. PAUP: Phylogenetic Analysis Using Parsimony, ver. 3.1. Computer program distributed by the Illinois Natural History Survey, Champaign, Illinois.

Takhtajan, A. 1980. Outline of the classification of flowering plants (Magnoliophyta). Bot. Rev. 46: 225–359.

Thorne, R. T. 1983. Proposed new realignments in the angiosperms. Nordic J. Bot. 3: 85–117.

Walker, J. W. & J. A. Doyle. 1975. The bases of angiosperm phylogeny: Palynology. Ann. Missouri Bot. Gard. 62: 664–723.

Webster, G. L. 1967. The genera of Euphorbiaceae in the southeastern United States. J. Arnold Arbor. 48: 303–430.

———. 1975. Conspectus of a new classification of the Euphorbiaceae. Taxon 24: 593–601.

———. 1984. *Jablonskia*, a new genus of Euphorbiaceae from South America. Syst. Bot. 9: 229–235.

———. 1987. The saga of the spurges: A review of classification and relationships in the Euphorbiales. J. Linn. Soc., Bot. 94: 2–46.

———. 1994. Synopsis of the suprageneric taxa of Euphorbiaceae. Ann. Missouri Bot. Gard. 81: 000–000.

———, L. Gillespie & J. Steyermark. 1987. Systematics of *Croizatia* (Euphorbiaceae). Syst. Bot. 12: 1–8.

Wiley, E. O. 1979. An annotated Linnean hierarchy, with comments on natural taxa and competing systems. Syst. Zool. 28: 308–337.

———. 1981. Phylogenetics. The theory and practice of phylogenetic systematics. John Wiley & Sons, New York.

PHYLOGENETIC RELATIONSHIPS OF *DIDYMOCISTUS* AND *HYMENOCARDIA* (EUPHORBIACEAE)[1]

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Abstract

The genus *Hymenocardia* has been placed either in Euphorbiaceae subfamily Phyllanthoideae or in its own family and then associated with the Urticales, particularly the Ulmaceae. However, the pollen exine wall of *Hymenocardia* lacks the microchanneled tectum, granular interstitium, and thin foot-layer of the Urticales. *Hymenocardia* instead has many palynological features found in the Phyllanthoideae and should be retained in the Euphorbiaceae in that subfamily. *Didymocistus*, which has scalelike foliar trichomes and exine sculpturing and ultrastructure similar to *Hymenocardia*, should be transferred from the Phyllanthoideae–Aporuseae to a position near *Hymenocardia*.

The relationships of *Hymenocardia* Wallich ex Lindley have been controversial ever since Airy Shaw (1965) segregated the genus as its own family, Hymenocardiaceae. Previous authors had placed *Hymenocardia* in the Euphorbiaceae with genera now included in subfamily Phyllanthoideae, either without special attention (Baillon, 1874; Bentham, 1880; Pax & Hoffmann, 1922, 1931), in a distinct tribe but with other genera (Hutchinson, 1969), or in a tribe (or subtribe) by itself (Mueller, 1866; Webster, 1975). Radcliffe-Smith (1973, 1987a) and Léonard & Mosango (1985) have also accepted the Hymenocardiaceae, though Webster (1967, 1975, 1987, 1994) has not. Léonard & Mosango (1985) and Radcliffe-Smith (1987b) reviewed the history of this controversy more completely.

Levin (1986a–c), studying leaf architecture and epidermal morphology, suggested that *Didymocistus* Kuhlm., a monotypic South American genus, was closely related to *Hymenocardia*. Webster (1975) had placed *Didymocistus* in the tribe Aporuseae of the Phyllanthoideae, following suggestions Kuhlmann (1940) made when he described the genus. (Note that Webster (1994) more recently treated the Aporuseae as subtribe Scepinae of the tribe Antidesmeae; for convenience we will continue to refer to this group as the Aporuseae.) Levin based his proposal on the absence in *Didymocistus* of marginal glands, enlarged tanniniferous epidermal cells, and anisocytic stomata, all synapomorphies of Aporuseae, and the presence in that genus and *Hymenocardia* of relatively organized leaf venation, which in turn linked these genera with some members of Phyllanthoideae tribe Phyllantheae.

We have undertaken a review of the morphological literature from a phylogenetic perspective with the goal of clarifying the relationships of these genera. We have also obtained new data on the pollen morphology and ultrastructure and foliar trichome anatomy of both genera for comparison with each other and other Euphorbiaceae. As we will show, these results lead us to conclude that *Didymocistus* and *Hymenocardia* are closely related members of the Phyllanthoideae.

Materials and Methods

We examined pollen of *Didymocistus chrysadenius* Kuhlm. (*Dodson & Torres 2961*, MO), *Hymenocardia acida* Tul. (*de Wilde 4044*, MO), and *H. ulmoides* Oliver (*Lebrun 2119*, MO) using light microscopy (LM), scanning electron microscopy (SEM), and transmission electron microscopy (TEM). Details of specimen preparation can be

[1] We thank the curators at MO and RSA/POM for allowing us to remove leaf fragments and pollen from collections in their care. Jon Blevitt, Kitty Huntley, and Nicki Watson helped with specimen preparation, sectioning, and photography.

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found in Levin & Simpson (1994, this issue) and Simpson & Levin (in press). The *Hymenocardia* species were selected to represent the two subgenera recognized by Léonard (1957).

We examined the foliar trichomes of *D. chrysadenius* (*Davidson 5356*, RSA) and *H. acida* (*Enti R.755*, RSA) using LM and SEM. Leaf fragments from dried herbarium specimens were first rehydrated at 60°C in 10% Aerosol OT for two days, then fixed and stored in F.A.A. (formalin/acetic acid/ethanol). For LM observations, rehydrated leaf fragments were embedded in paraffin following standard procedures; sectioned at 10 μm; stained with safranin O, fast green, and haematoxylin; and mounted. LM observations, photographs, and drawings were made using Nikon Microphot-FX photomicroscope equipped with a camera lucida. For SEM observations, the rehydrated leaf fragments were prepared and photographed following the same procedure used for the pollen (Levin & Simpson, 1994).

Results and Discussion

Those authors who have segregated *Hymenocardia* from the Euphorbiaceae have emphasized similarities with the Urticales, particularly Ulmaceae. For example, Airy Shaw (1965) noted that the male flowers, which lack both petals and a disk, are "decidedly 'Urticaceous' or 'Ulmaceous' in appearance," and Radcliffe-Smith (1987b) remarked that the anthers fold outward after anthesis like some Ulmaceae. The flowers of *Didymocistus* also lack both petals and a disk, as do flowers of many Euphorbiaceae and Ulmaceae. Given the striking reduction of the flowers, it is difficult to determine whether the similarities are due to common ancestry or convergence.

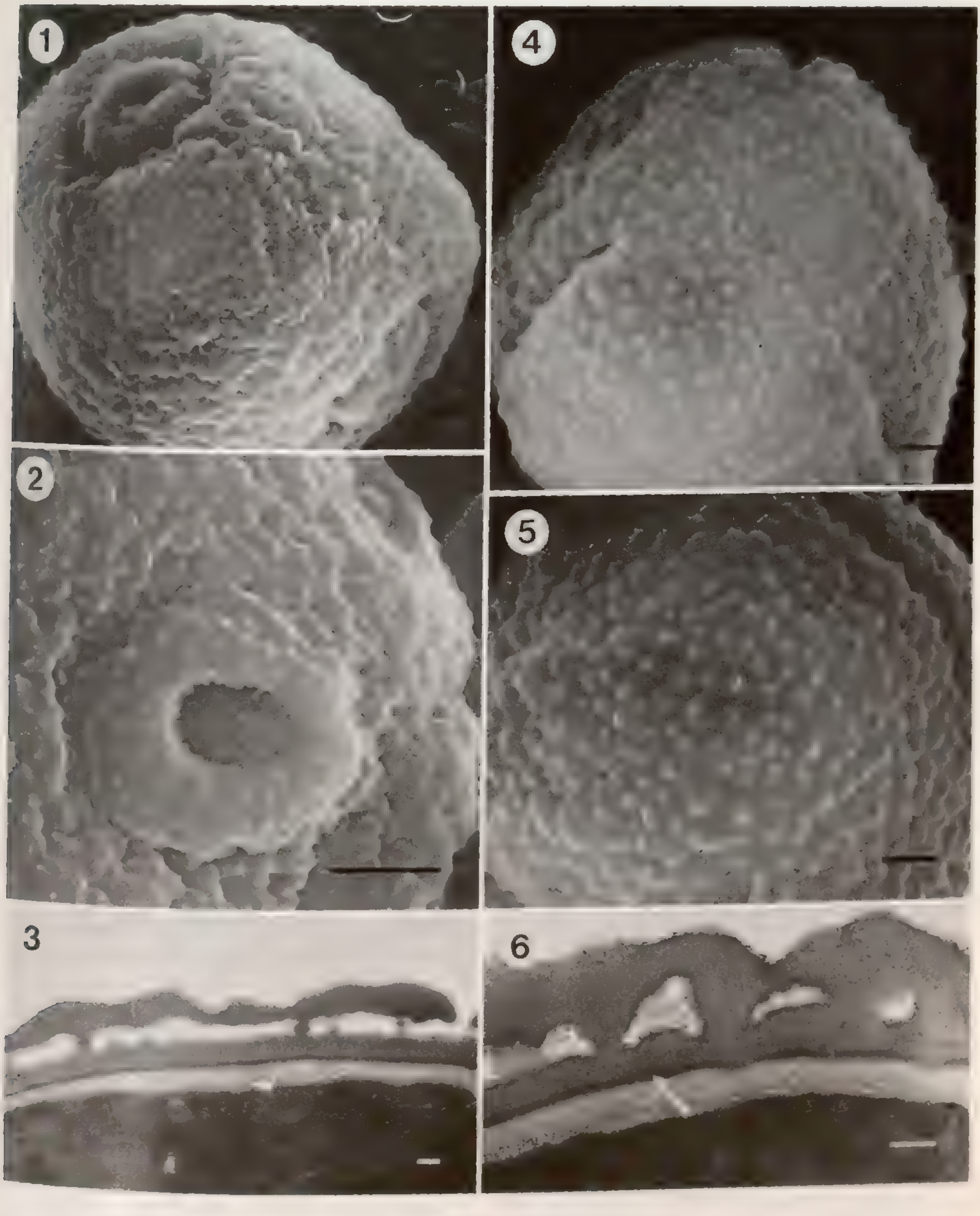
The winged fruits of *Hymenocardia* also resemble those of some Ulmaceae, notably *Holoptelea* Planchon (Airy Shaw, 1965). This resemblance is strictly superficial, however, because as Radcliffe-Smith (1987b) pointed out, the fruits of *Hymenocardia* are bilocular, flattened at right angles to the partition, and dehiscent, whereas fruits of *Holoptelea* and other samara-producing Ulmaceae are indehiscent and almost always unilocular. Furthermore, carpels of *Hymenocardia* are biovulate (like those of *Didymocistus* and other Phyllanthoideae), whereas carpels of Ulmaceae are uniovulate. Fruits of *Didymocistus* are bilocular and dehiscent, and conceivably could represent a transition between the trilocular dehiscent fruit found in most Phyllanthoideae and the unusual fruits of *Hymenocardia*.

Pollen morphology has also been cited as evidence for a relationship between *Hymenocardia* and the Ulmaceae. Both Punt (1962) and Köhler (1965), using LM, noted that the pollen of *Hymenocardia* is unlike that of any other Phyllanthoideae they examined (neither studied pollen of *Didymocistus*). Livingstone (1967) was the first to observe that the oblate triporate pollen is nearly indistinguishable from that of *Celtis* L. (Ulmaceae), at least with LM. Dechamps et al. (1985) examined *Hymenocardia* pollen using SEM. Comparison of both their photographs and ours (Figs. 1, 2) with published SEM photographs of Ulmaceae pollen (e.g., Zavada & Crepet, 1981; Zavada & Dilcher, 1986) reinforces the similarity between pollen of *Hymenocardia* and Ulmaceae, especially *Celtis*.

Our TEM studies demonstrate that this similarity, though striking, almost certainly is convergent. Zavada & Dilcher (1986) showed that the exine of Ulmaceae and related families has a microchanneled tectum, granular interstitium, and thin foot-layer, which appear to be synapomorphies of an advanced group of families. Exine ultrastructure of *Hymenocardia* pollen (Fig. 3) is like that of other Phyllanthoideae (see Levin & Simpson, 1994; Simpson & Levin, in press), however, with a homogeneous tectum, columellar interstitium, and moderately thick foot-layer. It is very unlikely that these character states would be found in a close relative of the Ulmaceae.

Exine sculpturing and structure of *Didymocistus* pollen (Figs. 4–6) is quite similar to that of *Hymenocardia*. Both have nearly identical rugulate sculpturing with minute outer spinules (Figs. 2, 5). Rugulate sculpturing apparently is a synapomorphy for these genera, because almost all Phyllanthoideae, including all Aporuseae and Phyllantheae as far as known, have reticulate sculpturing. Spinulose pollen is very rare in the Phyllanthoideae (Levin & Simpson, 1994) and may also be a synapomorphy of *Didymocistus* and *Hymenocardia*. Like other Phyllanthoideae, *Didymocistus* has a homogeneous tectum, columellar interstitium, and moderately thick foot-layer. The main difference between pollen of *Didymocistus* and *Hymenocardia* is that the apertures of *Didymocistus* are colporate (Fig. 4) whereas those of *Hymenocardia* are pororate (Figs. 1, 2). This change may reflect increased adaptation for wind pollination in *Hymenocardia*.

Wood characters also support retaining *Hymenocardia* in the Phyllanthoideae and placing it near *Didymocistus*. Unlike Ulmaceae, which have wood with non-septate fibers and well-developed axial parenchyma (Metcalfe & Chalk, 1950), *Hymenocardia* has wood with septate fibers and no axial xylem parenchyma (Dechamps et al., 1985;



FIGURES 1–6. *Hymenocardia acida* pollen (Figs. 1–3): *de Wilde 4044*, MO. *Didymocistus chrysadenius* pollen (Figs. 4–6): *Dodson & Torres 2961*, MO.—1, 2, 4, 5. Scanning electron micrographs.—3, 6. Transmission electron micrographs. Arrow in Figure 6 indicates endexine. Scale bars in 1, 2, 4, 5 = 1 μm; in 3 and 6 = 0.2 μm.

Mennega, 1987). Similar wood is found in genera of Phyllanthoideae with the derived '*Glochidion*-type' wood (Metcalfe & Chalk, 1950; Mennega, 1987), particularly the Phyllantheae, and in *Didymocistus* (Mennega, 1984, 1987), all of which also share vessel elements with simple perforate plates. In contrast, wood of the Aporuseae has non-septate fibers and abundant axial parenchyma, and generally has scalariform perforation plates (Mennega, 1984, 1987); these characteristics appear to be plesiomorphic for the Phyllanthoideae. Though a few vessel elements in *Didymocistus* wood have scalariform perforation plates, because this is the plesiomorphic condition it would not contradict a

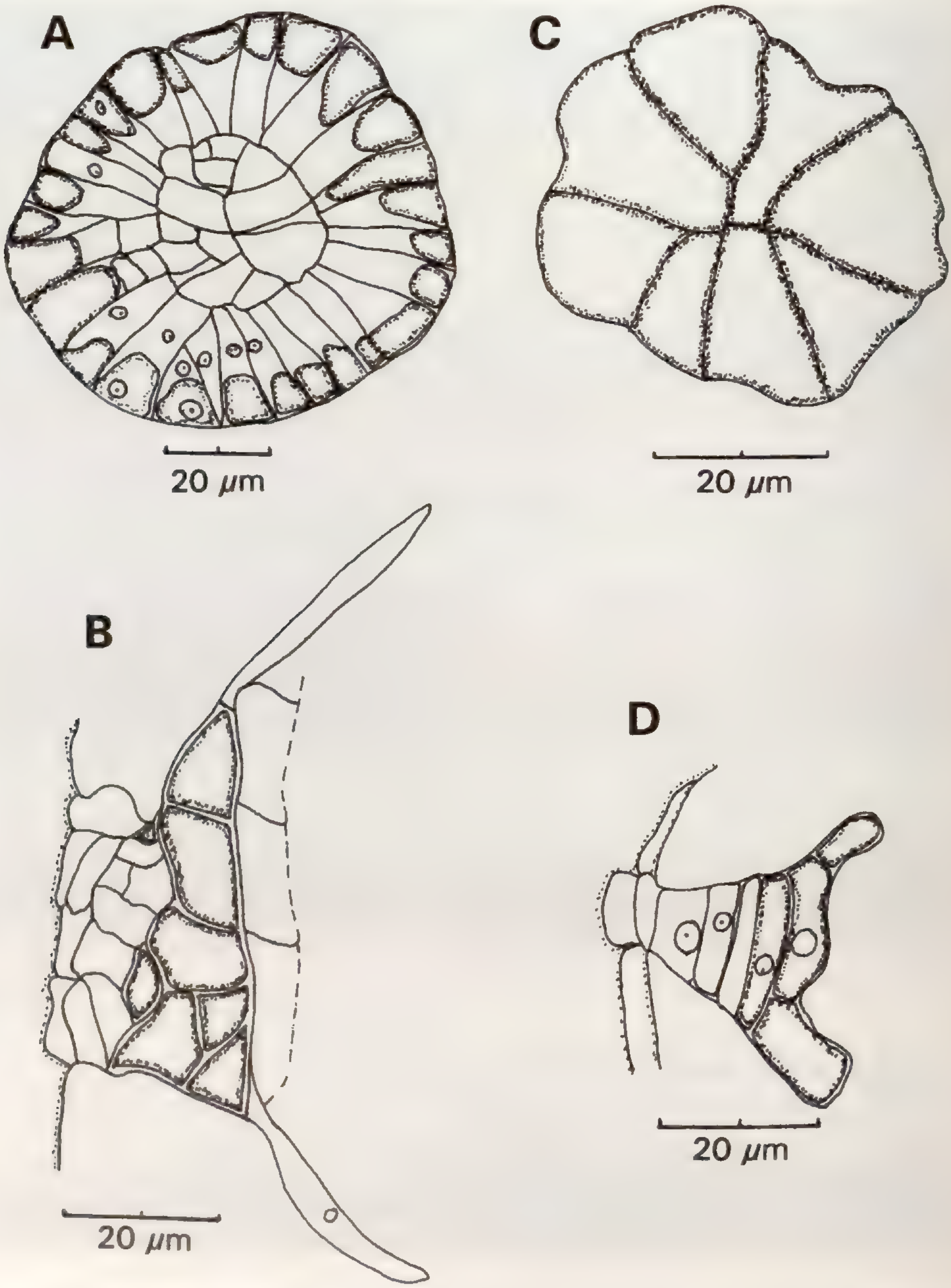


FIGURE 7. *Hymenocardia acida* leaf trichomes (Fig. 7A, B): *Enti R.755*, RSA. *Didymocistus chrysadenius* leaf trichomes (Fig. 7C, D): *Davidson 5356*, RSA.—A, C. Cross section through head.—B, D. Longitudinal section.

relationship to the Phyllantheae. As noted above, leaf architectural synapomorphies also unite *Didymocistus*, *Hymenocardia*, and some of the genera with '*Glochidion*-type' wood, particularly genera Webster (1975, 1994) placed in the tribe Phyllantheae (Levin, 1986a, c).

We also found that both *Hymenocardia* and *Didymocistus* have scalelike trichomes on the abaxial leaf surface (Fig. 7). These trichomes differ in size and structural details. In *Hymenocardia* (Fig. 7A, B) the trichomes have a multiseriate stalk and a head 77–102 μm in diameter consisting of a central region of more or less isodiametric cells and an outer region of radially-oriented cells, the

outermost of which have thickened walls. In *Didymocistus* (Fig. 7C, D) the trichomes have a uniseriate stalk and a head 40–51 μm in diameter consisting of about eight cells. Though somewhat different in structure, perhaps as a consequence of size, similar scalelike trichomes are otherwise unknown in the Phyllanthoideae and may be a synapomorphy linking *Didymocistus* and *Hymenocardia*.

Two additional lines of evidence argue that *Hymenocardia* belongs in the Phyllanthoideae. First, its ovules are anatropous and epitropous, bitegmic, crassinucellate, and inserted below a placental obturator (Baillon, 1858), a structure that is typical of the Euphorbiaceae (Webster, 1967) but different from the Urticales (Cronquist, 1981). Second, the chromosome number is $n = 13$ as in most Phyllanthoideae (Hans, 1973), a number unknown in the Ulmaceae (Cronquist, 1981). These data are unknown for *Didymocistus*.

Chemistry offers some additional evidence regarding the relationships of *Didymocistus*. Rundel & Levin (unpublished) have found that aluminum hyperaccumulation is a synapomorphy of the Aporuseae. *Didymocistus*, like all other Phyllanthoideae outside Aporuseae, does not hyperaccumulate aluminum.

Conclusions

The data we have reviewed here strongly suggest that *Hymenocardia* bears no relationship to the Ulmaceae and other Urticales. Pollen ultrastructure, wood anatomy, ovule structure, and chromosome number demonstrate that the similarities between *Hymenocardia* and some Ulmaceae, e.g., reduced flowers and rugulate, triporate pollen, result from convergence rather than common ancestry. In contrast, *Hymenocardia* is not strikingly different from many Euphorbiaceae subfamily Phyllanthoideae, and shares many similarities with *Didymocistus*. It is also clear that *Didymocistus* and the Aporuseae differ from each other in characters of pollen, wood anatomy, foliar morphology, and chemistry in such a way that a relationship between them is highly unlikely.

We included both *Didymocistus* and *Hymenocardia* in a cladistic analysis of selected Euphorbiaceae using characters of pollen, vegetative anatomy and morphology, and reproductive morphology (Levin & Simpson, 1994). Though we included too few Phyllanthoideae to say much about relationships within this subfamily, we did find that *Didymocistus* and *Hymenocardia* consistently formed a monophyletic group that was the sister group of *Margaritaria* L. f. and *Phyllanthus* L., two of the three Phyllantheae we included in that study (see Levin & Simpson, 1994, fig. 29). (The relationships of *Securinega* Comm. ex. A. L. Juss., the third member of Phyllantheae we studied, are ambiguous (Levin & Simpson, 1994; Webster, 1994).) Synapomorphies shared by *Didymocistus*, *Hymenocardia*, and the Phyllantheae include wood with simple perforation plates, septate fibers, and lacking axial parenchyma, and leaves with percurrent tertiary veins. Synapomorphies shared by *Didymocistus* and *Hymenocardia* include rugulate pollen sculpturing with minute spinules, highly organized higher-order leaf venation, scalelike foliar trichomes, and bilocular ovaries (the last two characteristics were not included in our cladistic analysis).

Given the data we have reviewed here and the results of our cladistic analysis, we conclude that *Didymocistus* and *Hymenocardia* are closely related and should be placed in their own tribe, the Hymenocardieae. This treatment was adopted by Webster (1994). The Hymenocardieae, in turn, should be placed near the Phyllantheae.

Literature Cited

Airy Shaw, H. K. 1965. Diagnoses of new families, new names, etc., for the seventh edition of Willis's "Dictionary." Kew Bull. 18: 249–273.

Baillon, H. 1858. Etude Générale du Groupe des Euphorbiacées. Victor Masson, Paris.

———. 1874. Euphorbiacées. Histoire des Plantes 5: 105–256. Hachette, Paris.

Bentham, G. 1880. Euphorbiaceae. *In:* G. Bentham & J. D. Hooker (editors), Genera Plantarum ad Exemplaria Imprimis in Herberiis Kewensibus Servata Definita, 3: 239–340. Lovell Reeve & Co., London.

Cronquist, A. 1981. The Evolution and Classification of Flowering Plants. Houghton Mifflin, Boston, Massachusetts.

Dechamps, R., M. Mosango & E. Robbrecht. 1985. Etudes systématiques sur les Hymenocardiaceae d'Afrique: la morphologie du pollen et l'anatomie du bois. Bull. Jard. Bot. Etat 55: 473–485.

Hans, A. S. 1973. Chromosomal conspectus of the Euphorbiaceae. Taxon 22: 591–636.

Hutchinson, J. 1969. Tribalism in the family Euphorbiaceae. Amer. J. Bot. 56: 738–758.

Kohler, E. 1965. Die Pollenmorphologie der Biovulaten Euphorbiaceae und ihre Bedeutung für die Taxonomie. Grana Palynol. 6: 26–120.

Kuhlmann, J. G. 1940. Especies novas equatoriais. Anais Reunião Sul.-Amer. Bot. 3: 78–86.

Leonard, J. 1957. Notes systématiques et cécidologiques sur les espèces du genre *Hymenocardia* Wall. (Euphorbiacées). Bull. Soc. Roy. Bot. Belgique 90: 15–21.

——— & M. Mosango. 1985. *Hymenocardiaceae. In:* P. Bamps (editor), Flore d'Afrique Centrale: Spermatophytes. Jardin Botanique National de Belgique, Brussels.

LEVIN, G. A. 1986a. Systematic foliar morphology of Phyllanthoideae (Euphorbiaceae). I. Conspectus. Ann. Missouri Bot. Gard. 73: 29–85.

———. 1986b. Systematic foliar morphology of Phyllanthoideae (Euphorbiaceae). II. Phenetic analysis. Ann. Missouri Bot. Gard. 73: 86–98.

———. 1986c. Systematic foliar morphology of Phyllanthoideae (Euphorbiaceae). III. Cladistic analysis. Syst. Bot. 11: 515–530.

——— & M. G. SIMPSON. 1994. Phylogenetic implications of pollen ultrastructure in the Oldfieldioideae (Euphorbiaceae). Ann. Missouri Bot. Gard. 81: 203–238.

LIVINGSTONE, D. A. 1967. Postglacial vegetation of the Ruwenzori Mountains in equatorial Africa. Ecol. Monogr. 37: 25–52.

MENNEGA, A. M. W. 1984. Wood structure of *Jablonskia congesta* (Euphorbiaceae). Syst. Bot. 9: 236–239.

———. 1987. Wood anatomy of the Euphorbiaceae, in particular of the subfamily Phyllanthoideae. J. Linn. Soc., Bot. 94: 111–126.

METCALFE, C. R. & L. CHALK. 1950. Anatomy of the Dicotyledons, 1st ed., Vol. 2. Oxford Univ. Press, Oxford.

MUELLER, J. 1866. Euphorbiaceae. *In:* A. P. de Candolle (editor), Prodromus Systematis Naturalis Regni Vegetabilis 15(2): 189–1261. Victor Masson, Paris.

PAX, F. & K. HOFFMANN. 1922. Euphorbiaceae–Phyllanthoideae–Phyllantheae. *In:* A. Engler (editor), Das Pflanzenreich, IV, 147. XV (Heft 81): 1–349.

——— & ———. 1931. Euphorbiaceae. *In:* A. Engler & K. Prantl (editors), Die Natürlichen Pflanzenfamilien, ed. 2, 19c: 11–233.

PUNT, W. 1962. Pollen morphology of the Euphorbiaceae with special reference to taxonomy. Wentia 7: 1–116.

RADCLIFFE-SMITH, A. 1973. A new variety of *Hymenocardia acida* (Hymenocardiaceae). Kew Bull. 28: 324.

———. 1987a. Euphorbiaceae (Part 1). *In:* R. M. Polhill (editor), Flora of Tropical East Africa. A. A. Balkema, Rotterdam.

———. 1987b. Segregate families from the Euphorbiaceae. J. Linn. Soc., Bot. 94: 47–66.

SIMPSON, M. G. & G. A. LEVIN. Pollen ultrastructure of the biovulate Euphorbiaceae. Int. J. Pl. Sci. (in press.)

WEBSTER, G. L. 1967. The genera of Euphorbiaceae in the southeastern United States. J. Arnold Arbor. 48: 303–430.

———. 1975. Conspectus of a new classification of the Euphorbiaceae. Taxon 24: 593–601.

———. 1987. The saga of the spurges: a review of classification and relationships in the Euphorbiales. J. Linn. Soc., Bot. 94: 2–46.

———. 1994. Synopsis of the genera and suprageneric taxa of Euphorbiaceae. Ann. Missouri Bot. Gard. 81: 33–144.

ZAVADA, M. S. & W. L. CREPET. 1981. Investigations of Angiosperms from the middle Eocene of North America: flowers of the Celtidoideae. Amer. J. Bot. 68: 924–933.

——— & D. L. DILCHER. 1986. Comparative pollen morphology and its relationship to phylogeny of pollen in the Hamamelidae. Ann. Missouri Bot. Gard. 73: 348–381.

A PALYNOLOGICAL STUDY OF CROTONOIDEAE (EUPHORBIACEAE)[1]

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Abstract

Pollen of 69 species representing 34 genera from 12 of the 13 tribes of Crotonoideae sensu Webster was examined in light microscopy (LM), scanning electron microscopy (SEM), and transmission electron microscopy (TEM). The pollen of the vast majority of the subfamily is inaperturate, and all Crotonoideae exines have a similar architecture: triangular supratectal elements attached to a network of muri having short or irregular columellae. These three components, triangular supratectal elements, muri, and modified columellae constitute the Croton structure. The triangular elements, designated subunits, can be psilate, striate, furrowed and ridged, or pitted, and with echinate, rounded, or long-attenuate apices; the subunits can be closely spaced or arrayed in more open configurations. A Croton sculpture refers to the presence of triangular sculpture elements, which may or may not have muri and modified columellae. Inaperturate grains have thin footlayers and thin endexines, whereas colpate pollen has both footlayer and endexine well developed; in porate grains, the footlayer and endexine appear intermediate between inaperturate and colpate. Tribes Micrandreae (*Hevea*, *Micrandra*, *Micrandropsis* examined) and Adenoclineae (*Adenocline*, *Ditta*, *Glycydendron*, *Endospermum*, *Klaineanthus*, *Tetrorchidium*) are 3-colpate and probably primitive, having retained not only apertures but (prominent) footlayers and endexines as well; Manihoteae (*Manihot*, *Cnidoscolus* examined) and Gelonieae (*Suregada*) are porate. The thicker aperturate exines, especially in the colpate grains, may be linked with retention of apertures. The remaining 22 genera examined, including the two largest, *Croton* and *Jatropha*, have inaperturate pollen. A thin footlayer/endexine also occurs in Oldfieldioideae, and a tectum with triangular elements is found in some Acalyphoideae. In both morphology and exine structure, the pollen of Crotonoideae closely resembles the (porate) pollen of Thymelaeaceae.

In a family as large and diverse as Euphorbiaceae (300 genera, 7500 species), variation in pollen morphology/structure would be expected. In fact, there is a striking array of pollen diversity as demonstrated by Punt's (1962) classic study of Euphorbiaceae in which numerous pollen types are illustrated with line drawings. Even genera, e.g., *Phyllanthus* (Punt, 1987) and *Zimmermannia* (Poole, 1981), can be highly variable in pollen morphology, thus casting some doubt on the taxonomic value of pollen data in this family.

In his 1962 study, Punt followed the treatment of Euphorbiaceae in Pax & Hoffmann (1931), recognizing only two subfamilies, Crotonoideae and Phyllanthoideae. Later, he (1987) considered Webster's (1975) system that elevated three Crotonoideae tribes to subfamily status, Oldfieldioideae, Acalyphoideae, and Euphorbioideae, in addition to Phyllanthoideae and the remaining Crotonoideae, to represent the best concept of the family to date. In part, pollen data support Webster's classification (see Discussion).

By segregating the above three tribes from Crotonoideae, the remaining members of this subfamily form a much more natural alliance that may or may not be monophyletic.

The Crotonoideae, sensu Webster, comprise 13 tribes and approximately 73 genera, of which three, *Croton*, *Jatropha*, and *Manihot*, account for half of the 2000 species. Crotonoideae now appear to be the exception to pollen diversity and have surprisingly uniform pollen morphology, united by the croton-pattern. This term apparently originated with Erdtman (1952, 1966: 173) for pollen with a sexine that "consists of well defined, regularly arranged excrescences (triangular or more or less circular in cross section), supported (always?) by a baculate, baculoidate, or spongy layer." He noted that most of the croton-pattern pollen was nonaperturate and spheroidal. Punt (1962) examined at

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least 50 species that are referable to the reduced Crotonoideae, all of which have a pollen type that he designated as the Croton Configuration. This configuration was delimited by (1962: 47): "Croton-pattern present. Structure elements on the tectum are usually clavae but can also be echinae, baculae etc. Sometimes the structure elements are located on ridges (e.g., *Croton matourensis*, *Manihot saxicola*). Tectate." Punt reserved "Croton type" for the inaperturate grains, "Manihot type" for the periporate, "Klaineanthus type" for tricolpate, "Hevea type" for tricolpate with opercula, etc. In view of the results presented here, both Erdtman's and Punt's concept of a Croton pattern in Euphorbiaceae pollen have to be amended.

Inaperturate pollen is an unusual condition in the angiosperms, and Crotonoideae have at least 1500 species whose pollen lacks preformed thin areas. In an effort to expand the limited information from light microscopy, which was all that was available to Erdtman (1952) and Punt (1962), a study emphasizing electron microscopy was initiated. The presence of 3-colpate and pantoporate pollen in Crotonoideae provides a rare opportunity to compare exine structure modifications between inaperturate and aperturate grains of related taxa. Sixty-nine species were examined in light microscopy (LM) and scanning electron microscopy (SEM), and 33 of the 69 were embedded and examined in transmission electron microscopy (TEM). In addition, representative species from Acalyphoideae, Euphorbioideae, Phyllanthoideae, and Oldfieldioideae were examined and are briefly discussed. A potentially close relationship between Crotonoideae and Thymelaeaceae (Nowicke, Skvarla & Patel, unpublished data) based on pollen similarities is also discussed. For ease of reference, examples of some subfamilies and Thymelaeaceae are illustrated.

The thrust of this effort is to expand the pollen data set for Crotonoideae and not to provide an exhaustive search of the literature (see Punt, 1987, for references to that date).

All species examined, with voucher data and figure number(s), are given in Table 1.

Materials and Methods

Anthers were removed from herbarium specimens, and pollen for all preparations was first acetolyzed as outlined by Erdtman (1966), but heating time was reduced from two minutes to one in an attempt to alleviate collapse and fragmentation. This reduction had varying degrees of success.

Glass slides for LM were made with glycerin jelly and sealed with paraffin.

For SEM, acetolyzed pollen was pipetted onto specimen stubs in 50% alcohol and allowed to dry. After coating with carbon and then gold-palladium, the samples were examined and photographed in a Hitachi 911b scanning electron microscope.

For TEM, acetolyzed pollen was incorporated into 2% agar, fixed with osmium tetroxide, stained with uranyl acetate, and embedded in Spurrs or in L. R. White Acrylic Resin. After sectioning with diamond knives the sections were stained with lead citrate, and then examined and photographed with a JEOL 1200EX transmission electron microscope.

Electron micrographs and glass slides are deposited at the Palynological Laboratory, National Museum of Natural History, Smithsonian Institution.

Results

The Results are organized as follows: a Crotonoideae pollen description; characterization of exine structure for inaperturate, porate, and colpate pollen; the range of variation in tecta, subunits, muri, columellae, footlayers, and endexines; and a brief discussion of pollen in each of the 12 tribes examined.

Crotonoideae, figures 1–88

Pollen mostly spheroidal, occasionally subprolate; inaperturate, sometimes pantoporate, more rarely 3-colpate, or very rarely 3-colporate; the tectum incomplete and consisting of the distal muri, the lumina usually with shallow free columellae globules of ektexine, the muri with triangular or rounded-triangular supratectal elements designated as subunits, the subunits frequently forming continuous (triangular) arrays, their surface psilate, pitted, striate, or furrowed and ridged, their apices echinate, rounded, flat, or attenuate, the subunits densely spaced or arrayed in more open configurations, absent in one species. In TEM, the endexine mostly very thin, irregular and discontinuous, consisting of granules or sometimes lamellae, or (in porate grains) the endexine thin but more consistent, or more rarely (in colpate grains) the endexine forming a discrete layer and sometimes detached (after acetolysis); the footlayer mostly very thin, irregular and discontinuous, occasionally seeming to consist of granules, or sometimes (in porate grains) uneven but consistently present, or more rarely (in colpate grains) the footlayer prominent and continuous; the supporting columellae (in in-

aperturate grains) short but well defined, sometimes appearing to be in two rows, or (in porate grains) the columellae more elongate but irregular, or more rarely (in colpate grains) the columellae granular; the tectum consisting of the distal muri, the muri thin to thick, the subunits (as demonstrated in tangential section) triangular to rounded-triangular, with or without grooves.

Although variation in the supratectal elements makes some pollen distinctive, all Crotonoideae examined here (Table 1), inaperturate and aperturate, are fundamentally similar: triangular supratectal elements are attached to muri having short or irregular/granular columellae. The presence of triangular supratectal elements, referred to as subunits, their attachment to a network of muri, and the modified columellae, constitute the Croton structure. This definition incorporates information from transmission electron microscopy not available to either Erdtman (1952) or Punt (1962). Radial thin sections show that the subunits are always attached to muri, e.g., Figures 11, 14, 17, 23, 26, 31, 36, 39, 41 inset, 47 inset, 63, 69, 72, 75, 82, and 88; and tangential sections show that the basic shape of the subunits in cross section is triangular or rounded-triangular, e.g., Figures 6, 8, 13, 18, 21, 27, 33, 37, 47, 65, 79, and 85.

A Croton sculpture refers only to the presence of triangular supratectal elements.

INAPERTURATE POLLEN, FIGURES 34–88

The inaperturate exines can be further characterized by: a footlayer/endexine that, even taken together, usually comprise a very thin layer (e.g., Figs. 36, 44, 54, 63, 78, 82, 83); and a thick, uniformly distributed intine. This exine structure can be demonstrated in tangential section, e.g., *Jatropha hastata* (Fig. 37) and *Ostodes zeylanica* (Fig. 47). In both, the outermost solid discrete objects are the subunits cut at various levels and angles, (proceeding inward) the distinctly smaller circular objects (wavy arrows) are free columellae and/or globular masses of ektexine in the lumina, next are the more or less solid bars (arrows) of the restricted muri (restricted because in these two species the muri are thin and occupy only a small proportion of the area), and in the center of the sections are the paired supporting columellae (arrowheads) organized into lines, as well as more free columellae cut closer to the base. Radial sections of *J. hastata* (Fig. 36) and *O. zeylanica* (Fig. 47 inset) confirm the thinness of the muri, as well as demonstrate the thin footlayer/endexine characteristic of most inaperturate Crotonoideae.

PORATE POLLEN, FIGURES 25–33

One of the porate tribes, Manihoteae (Figs. 25–30), has irregular, sometimes elongate, columellae, an uneven yet recognizable footlayer, and a thin endexine. However, only one species of *Manihot* (Figs. 26, 27) and one of *Cnidoscolus* (Fig. 29 inset) were examined in thin section and any structural characterization is a preliminary one.

The exine of the second porate tribe, Gelonieae (Figs. 31–33), has a threadlike footlayer/endexine and is similar to the inaperturate grains (see discussion of tribe).

COLPATE POLLEN, FIGURES 1–24

The exines of the colpate tribes, Micrandreae (Figs. 1–9) and Adenoclineae (Figs. 10–24), are distinguished by well-developed footlayers (e.g., Figs. 3, 6, 11, 13, 14, 17, 18, 23), a recognizable endexine (e.g., Figs. 3, 11, 14, 20, 23), at least under the colpi (e.g., Fig. 17), and mostly granular columellae (e.g., Figs. 6, 18, 23; unpublished data).

POLLEN MORPHOLOGY/EXINE STRUCTURE

At most, the Crotonoideae have an incomplete tectum, which consists only of the outer muri, i.e., the fused distal margins of the columellae. The attached subunits are considered sculpture.

Subunit refers to the triangular supratectal elements attached to the muri. Their fundamental shape in cross section is triangular, and these elements form or can form a continuous triangular array, e.g., Figures 25, 28, 62, and 67. Although the subunits in some grains do not appear triangular in SEM, tangential sections that cut across numerous subunits demonstrate a triangular or at least rounded-triangular shape, e.g., Figures 6, 8, 13, 18, 21, 33, 37, 47, 65, 85. The subunits can be modified by striations, e.g., Figures 24, 64, 66, and 81, or furrows and ridges, e.g., Figures 43, 48, and 70. Their apices can be echinate, e.g., Figures 14, 15, 20, 23, and 55, long attenuate, e.g., Figures 43, 53, 54, and 70, or simply rounded, e.g., Figures 31, 35, 36, 68, and 69, or even flat, e.g., Figures 25 and 26. Occasionally two or three subunits fuse.

In some Crotonoideae the muri are well developed, e.g., Figures 8, 18, 38, and 39; in others they are thin, e.g., Figures 41, 78, 79, and 82.

TABLE 1. Species examined, voucher data, and figure number if illustrated. All collections US unless indicated otherwise.

Euphorbiaceae			
Subfamily Crotonoideae			
Tribe 1. Micrandreae			
Micrandra elata Müll. Arg.	*Haught 1289*	Colombia	
M. kubeorum R. E. Schult.	*Schultes & Cabrera 13922*	Colombia	4
M. lopezii R. E. Schult.	*Tillet et al. 45050*	British Guiana	5, 6
M. minor Benth.	*Schultes & Cabrera 13820*	Colombia	
M. siphonioides Benth.	*Schultes & Lopez 8700*	Brazil	1–3
Micrandropsis scleroxylon W. A. Rodrigues	*Rodrigues et al. 6961*, NY	Brazil	7
	Rodrigues & Loureiro 9520, MO	Brazil	
Hevea guianensis Aubl.	*Asplund 13299*	Peru	8, 9
Tribe 2. Adenoclineae			
Adenoline bupleuroides (Meisn.) Prain	*Rogers 24550*	Natal	10–12
Ditta myricoides Griseb.	*Ekman 12802*	Hispaniola	13–15
Glycydendron amazonicum Ducke	*Black 148*	Brazil	18
Klaineanthus gaboniae Pierre ex Prain	*Zenker 583*	Cameroon	16, 17
Tetrorchidium rubrivenium Poepp.	*Patino 556*	Colombia	19–21
Endospermum diadenum (Miq.) Airy Shaw	*Krukoff 4109*, MO	Sumatra	
E. formicarium Becc.	*Floyd 3452*	New Britain	24
E. moluccanum Becc.	*Havel 15409*, MO	New Guinea	
E. ovatum Merr.	*Rojo 299*, MO	Philippines	
E. peltatum Merr.	*Sulit PNH 22900*	Philippines	22, 23
	Feniz 479	Philippines	
	Merritt 6891, MO	Philippines	
Tribe 3. Manihoteae			
Cnidoscolus angustidens Torr.	*Gentry 21176*	Mexico	
C. maculatus (Brandegee) Pax & K. Hoffm.	*Carter & Reese 4569*	Mexico	
C. rotundifolius (Müll. Arg.) McVaugh	*J. & M. Breckon 1295*	Mexico	29
C. sinaloensis Breckon	*Breckon & Webster 947*	Mexico	inset 29, 30
Manihot aesculifolia (Kunth) Pohl	*McVaugh 15355*	Mexico	25–27
M. brachyloba Müll. Arg.	*Haught 1664*	Colombia	
M. esculenta Crantz	*Fosberg 32263*	Carolina Islands	
M. grahami Hook.	*Renvoize et al. 3177*	Argentina	
M. irwinii D. J. Rogers & Appan	*Irwin et al. 34338*	Brazil	
M. marajoara Huber	*Huber s.n.*, Apr. 1908	Brazil	
M. pilosa Pohl	*Maxwell & Wasshausen 19774*	Brazil	28
M. pentaphylla Pohl	*Irwin et al. 34019*	Brazil	
M. pringlei S. Watson	*Pringle 3826*	Mexico	
M. tweediana Müll. Arg.	*Rojax s.n.*, Nov. 1933	Brazil	
M. tripartita (Spreng.) Müll. Arg. emend. D. J. Rogers & Appan	*Irwin et al. 18650*	Brazil	
M. violacea Pohl	*Heringer 18246*	Brazil	
Tribe 4. Gelonieae			
Suregada glomerulata (Blume) Baill.	*Ahern s.n.*, 1901	Philippines	31–33

TABLE 1. Continued.

Tribe 5. Jatropheae			
Deutzianthus tonkinensis Gagnep.	*Petelot 6388*	Vietnam	34
Jatropha cinerea (Ortega) Müll. Arg.	*Wiggins 16117*	Mexico	
J. glandulifera Roxb.	*Nowicke & Jayasuriya 386*	Sri Lanka	
J. hastata Jacq.	*Lundell 1577*	Yucatan	35–37
J. podagrica Hook.	*Blackbern E10*	Caroline Island	
Tribe 6. Elateriospermeae			
Elateriospermum tapos Blume	*Suvarnakoses 1872*	Thailand	38, 39
Tribe 7. Codiaeae			
Baliospermum axillare Blume	*Nicolson 2870*	Nepal	
Codiaeum variegatum (L.) Blume	*Calderon 1339*	El Salvador	40, 41
Dimorphocalyx luzoniensis Elmer	*Andaya s.n.*, 18 Mar. 1949	Philippines	45
Ostodes zeylanica Müll. Arg.	*Jayasuriya & Bandaranayake 1761*	Sri Lanka	46, 47
Pantadenia adenanthera Gagnep.	*Poilane 15385*, A	Cambodia	42
Pausandra densiflora Lanj.	*Ducke 1860*	Brazil	48
Sagotia racemosa Baill.	*Prance et al. 22670*	Brazil	43, 44
	Mexia 6051, A	Brazil	
Tribe 8. Trigonostemoneae			
Tribe 9. Ricinocarpeae			
Alphandia furfuracea Baill.	*Kajewski 809*	New Hebrides	49
Beyeria leschenaultii (DC.) Baill.	*Muir 1130*	Australia	52–54
Ricinocarpos bowmannii F. Muell.	*Boorman 17155*	Australia	
	Boorman s.n.	Australia	51
R. glaucus Endl.	*Helms s.n.*	Australia	50
R. stylosus Diels	*Webster 18714*, DAV	Australia	55
Bertya gummifera Planch.	*Johnson & Constable 16024*	Australia	56, 57
Tribe 10. Crotoneae			
Croton argyratus Blume	*Toroes 5241*	Sumatra	
C. balsamifer L.	*Smith 10452*	West Indies	60
C. californicus Müll. Arg.	*Wheeler s.n.*, 16 Nov. 1929	California	
C. draco Schltr.	*Salazar s.n.*, 11 Mar. 1913	Mexico	62, 63
C. floribundus Spreng.	*Mexia 5292*	Brazil	61
C. lachnocarpus Benth.	*Chun 6261*	China	
C. matourensis Aubl.	*Arch 8209*	Brazil	58, 59
C. mutisianus HBK	*Uribe 1322*	Colombia	
C. pyramidalis Donn. Sm.	*Dwyer 11073*	Belize	64
C. texensis Müll. Arg.	*White s.n.*, 26 Aug. 1946	Nebraska	65, 66
Tribe 11. Joannesieae			
Annesijoa novoguineensis Pax & K. Hoffm.	*Brass 32333*	New Guinea	70 72
Joannesia princeps Vell.	*Macedo 5335*	Brazil	67–69
Tribe 12. Aleuritideae			
Ricinodendron rautanenii Schinz	*Gibson 19*	Angola	76–79
Aleurites fordii Hemsl.	*Peterson 2805*	Argentina	73–75

TABLE 1. Continued.

Tribe 13. Neoboutonieae			
Anomalocalyx uleanus (Pax & K. Hoffm.) Ducke	*Ducke 64*	Brazil	80–82
Grossera major Pax	*Zenker 469*	Cameroon	83, 84
Crotonogyne argentea Pax	*Zenker 3078*	Cameroon	85–88
Subfamily Phyllanthoideae			
Drypetes lateriflora (Sw.) Krug & Urb.	*Contreras 1788*	Guatemala	
Phyllanthus acuminatus Vahl	*Standley 23316*	El Salvador	96
P. saffordii Merr.	*Fosberg 46286*	Guam	
P. simplex Retz.	*Toroes 4319*	Sumatra	
Flueggea flexuosa Müll. Arg.	*Wenzel 67*	Philippines	
Subfamily Oldfieldioideae			
Hyaenanche globosa (Gaertn.) Lamb. & Vahl	*Godfrey SH-1257*	South Africa	
Longetia buxoides Baill.	*Baumann 14418*	New Caledonia	92, 93
Subfamily Acalyphoideae			
Dalechampia humilis Müll. Arg.	*Hernger & Rizzini 17544*	Brazil?	89–91
D. dioscoreifolia Poepp. & Endl.	*Allen 5342*	Costa Rica	
Galearia celebica Koord.	*Brass 29233*	New Guinea	
G. filiformis (Blume) Pax	*Rahmat Si Boeea 7927*	Sumatra	
G. fulva (Tul.) Miq.	*J. & M. Clemens 3528*	Vietnam	
G. phlebocarpa (R. Br.) Miq.	*Rahmat Si Toroes 4429*	Sumatra	
	Rahmat Si Toroes 4892	Sumatra	
Macaranga denticulata Müll. Arg.	*Collins 1119*	Thailand	
M. griffithiana Müll. Arg.	*Sinclair 4990*	Malaya	
M. tanarius (L.) Müll. Arg.	*Rabil 338*	Thailand	
Microdesmis casearifolia Planch.	*Lei 514*	China	
M. pierlotiana J. Léonard	*Troupin 3549*	Congo	
M. puberula Planch.	*Baldwin 9058*	Liberia	
Omphalea diandra L.	*Irwin et al. 48498*	Guiana	
Panda oleosa Pierre	*Hladik s.n.*, 12 Nov. 1971	Gabon	
	Hall & Amponsah 46547	Ghana	
Subfamily Euphorbioideae			
Euphorbia pulcherrima Willd.	*Wheeler 12310*	Sri Lanka	94, 95
Hippomane mancinella L.	*Killip 41829*	Florida	
Mabea montana Müll. Arg.	*Standley 25156*	Panama	
Thymelaeaceae			
Gnidia glauca (Fresen.) Gilg	*Hoogland 11563*	Ceylon	101
Gyrinopsis cumingiana Decne.	*Ramos s.n.*, Jul.–Aug. 1915	Philippines	97, 98
Pimelea ligustrina Labill.	*Constable 45248*	New South Wales	102
P. prostrata (J. R. Forst. & G. Forst.) Willd.	*Anderson 186*	New Zealand	100
Schoenobiblus grandifolia Urb.	*Cowan 1548*	Tobago	99

In the Ricinocarpeae (Figs. 49–57), the muri appear to be reduced (see discussion of tribe).

The supporting columellae are variable, but in most inaperturate Crotonoideae they are short and many appear to be in two rows, e.g., Figures 37, 41 inset, 47, 54, 57, 78, and 83. All Adenoclineae and most Micrandreae have granular columellae (Figs. 6, 17, 23; unpublished data).

In the exines of inaperturate Crotonoideae, the footlayer and endexine are frequently so thin they cannot be distinguished from each other—at the proximal boundary of the columellae there are small granules above and below a "thread of exine," e.g., Figures 44, 59, 78, 82, and 83. Sometimes all the granules have the same electron density (Fig. 44). In a few taxa, a very thin lamellate endexine is present (Figs. 54, 57).

The footlayer of Adenoclineae (Figs. 10–24).

Elateriospermeae (Fig. 39), and some Micrandreae (Figs. 3, 6), is uniformly well-developed, whereas in the single species of the porate *Manihot* examined in thin section (Fig. 26), it is irregular.

Adenoclineae and Micrandreae have an endexine layer, at least beneath the apertures, although in Adenoclineae it frequently separates from the ektexine (Figs. 11, 14, 20, and 23). In Manihoteae, the endexine forms a thin consistent layer in *Cnidoscolus sinaloensis* and a thicker, but sometimes discontinuous, one in *Manihot aesculifolia* (Fig. 26).

Because of the reduced heating time in the acetolysis procedure (see Materials and Methods), some inaperturate pollen retained part, if not all, of the cytoplasmic contents and intine (Figs. 47 inset, 72, and 88).

The inaperturate Crotonoideae are known to have a very thick intine layer throughout the grain, a condition that Thanikaimoni et al. (1984) referred to as omniaperturate (in aperturate grains, a thick intine is usually present only under the apertures). In some inaperturate Crotonoideae, the acetolyzed exines have extensive surface areas where the wall consists of only a thin granular endexine/footlayer, e.g., Figures 36, 44, 59, 63, 75, 78, 82, and 83. The thick intine (Thanikaimoni et al., 1984: figs. 14, 15) may provide some mechanical/structural support, partially compensating for the extreme reduction of footlayer and endexine.

TRIBAL DESCRIPTIONS

Micrandreae, Figures 1–9

The seven species (Table 1) examined in the Micrandreae are 3-colpate. *Micrandra lopezii* (Figs. 5, 6), *M. siphonioides* (Figs. 1–3), and *Hevea guianensis* (Figs. 8, 9) were examined in thin section. *Micrandra* has a recognizable, mostly continuous, granular/lamellate endexine and a prominent footlayer. In radial sections of *M. lopezii*, the subunits are elongate, the muri very thin, and the columellae consist of a very thin granular layer—the proportion of the tangential section (Fig. 6) that each component occupies reinforces this characterization. In *M. siphonioides*, the muri appear obvious in SEM (Fig. 1) but not in TEM, and the columellae, while prominent, are irregular. This species is one of the very few in Crotonoideae that lack a Croton sculpture. In *M. kubeorum* (Fig. 4) the subunits are very irregular, and while muri are not demonstrated in Figure 4, they are in other SEMs of this sample (G. Webster, unpublished data). A fourth species, *M. elata*, examined only in SEM, has a tectum with triangular subunits, much like those illustrated in Figures 25, 28, and 62. A more extensive examination of *Micrandra* is warranted.

Micrandropsis (Fig. 7) also has a modified sculpture—the subunits are finely divided or very reduced, and the network of muri is irregular.

Hevea guianensis (Figs. 8, 9) has very small supratectal subunits, a finer network of muri with smaller lumina (compare Fig. 6 with Fig. 8; the latter is illustrated at a magnification five times greater than the former). In radial section, this species has a continuous endexine, an irregular but recognizable footlayer, and granular columellae.

Adenoclineae, Figures 10–24

Ten species representing six genera were examined. The 3-colpate grains of Adenoclineae have a distinctive yet remarkably uniform exine: a well-developed endexine (Fig. 17), frequently detached after acetolysis (Figs. 11, 14, 20, 23), a prominent footlayer (Figs. 11, 13, 14, 17, 18, 23), granular columellae (Figs. 17, 18, 23), and mostly thick muri (Figs. 14, 18, 21, 23). In addition, *Ditta*, *Endospermum*, *Glycydendron*, *Klaineanthus*, and *Tetrorchidium* have striate subunits with echinate apices. *Tetrorchidium rubrivenium* has been reported as 3-colporate (Punt, 1962), but only 3-colpate grains were found in the collection examined here (Table 1). *Klaineanthus*, however, is 3-colporate as demonstrated in Figure 16 and confirmed in LM. A few tetrads occurred in *Endospermum peltatum*. In thin section, *E. formacarium* is very similar to the exine portrayed in Figure 23 of *E. peltatum*.

In LM, the Adenoclineae can be easily distinguished from all other Crotonoideae by their colpi and thick exines—a prominent footlayer and thick, elongate or deep subunits. The deep subunits are especially noticeable in *Ditta* and *Tetrorchidium*.

These thick exines may be correlated with the development or retention of apertures since such walls could prove difficult to rupture in the germination process, and the increased pressure might be lethal to the sperm nuclei.

Manihoteae, Figures 25–30

Cnidoscolus and *Manihot* are characterized by large pantoporate (*M. tweediana* may be excepted) pollen. Only two species, one in *Manihot* and one in *Cnidoscolus*, were examined in TEM and any structural characterization is premature. *Manihot* has substantial muri, columellae that are irregular/granular yet collectively form a significant com-

ponent, an irregular but recognizable footlayer, and a discontinuous endexine (Figs. 26, 27). The wall structure of *Cnidoscolus* (Fig. 29 inset) is similar to *Manihot*, but on a smaller scale—it has a thin continuous footlayer and thin discontinuous endexine, and irregular/granular columellae. Like Micrandreae and Adenoclineae, the presence/retention of apertures appears correlated with thicker exines.

In *Manihot*, the subunits are conspicuously triangular, i.e., their flat or slightly rounded distal wall does not mask or detract from the triangular shape as do echinate or attenuate apices (as well as furrows and ridges). *Manihot tweediana* is unusual in that some grains appeared 15-pantocolpate (5-5-5) and/or 15-pantoporate.

Gelonieae, Figures 31–33

Suregada, the only genus in this tribe, comprises perhaps 40 species found in the warmer regions of the Old World. The pollen is of interest because it is porate, yet has an exine structure more characteristic of inaperturate pollen. The pores of *Suregada glomerulata* are small and even after acetolysis they retain a poorly defined aperture cover of smaller subunits (the term operculum is not appropriate because the margins are not defined). As a result, the pores are not conspicuous in SEM (arrows, Fig. 32). In thin section, columellae are difficult to identify—frequently there is an empty space between the muri and the threadlike footlayer/endexine (Fig. 31), or the muri are very thick and in direct contact with the footlayer/endexine. In tangential section, the free columellae or ektexine globules appear as black dots organized in circular groups (Fig. 33). The footlayer and endexine are extremely thin (Fig. 31), and even near the apertures the endexine remains thin. In the SEM preparation, there were threadlike, acetolysis-resistant filaments aggregating some of the sample into small groups of grains, usually no more than half dozen.

All remaining tribes have inaperturate pollen.

Jatropheae, Figures 34–37

In this tribe, only one species, *Jatropha hastata* (Figs. 35–37), was examined in thin section, but the structure is typical of other inaperturate Crotonoideae. The subunits are rounded-triangular in front view, the muri very thin, and the columellae short and irregular. Both footlayer and endexine together constitute only a thread with occasional small granules.

Dehgan & Webster (1979), in an infrageneric study of *Jatropha*, illustrated the pollen of 12 species in SEM (plates XXVII–XXIX), documenting the thin muri as well as supratectal subunits with striations; smooth subunits are present only in *Jatropha* subg. *Jatropha* sect. *Peltatae*.

Elateriospermeae, Figures 38–39

The exine of *Elateriospermum* can be distinguished from other inaperturate Crotonoideae by a well-developed, continuous footlayer and thick muri, both easily recognizable in LM. In some sections, columellae appear to hang from the muri. In SEM, there are some grains with one or two very small openings, probably a lumen without a footlayer. The radial section in Figure 39 illustrates a possible aperture—the gradual thinning of the footlayer and the size reduction of the subunits indicate a preformed opening, not a mechanical break in the exine; and, although not visible in the print in Figure 39, there is a very thin, less electron-dense endexine under the narrow footlayer. Given the thick footlayer, which could make germination difficult, the presence of apertures is not unexpected.

Codiaeae, Figures 40–48

This tribe reflects its large size, some 20 genera, in the subunit variation (Figs. 40, 42, 43, 46, 48). With the exception of *Pantadenia adenanthera* (Fig. 42), all remaining taxa examined (Table 1) have striate, furrowed, or ridged subunits. *Codiaeum variegatum* (Figs. 40, 41) has large lumina with free columellae/ektexine globules. *Pantadenia adenanthera* (Fig. 42) also has large lumina, but the actual muri are obscure. *Sagotia racemosa* (Figs. 43, 44) has subunits with long-attenuate tips (Fig. 43) and a footlayer/endexine (Fig. 44) that appears to consist of small granules above and below a thread of exine. Another collection of this species (Table 1) has large lumina similar to *Croton matourensis* (Fig. 58). The identification of both collections was verified. *Ostodes zeylanica* (Figs. 46, 47) has rounded, faintly grooved subunits with the widest part above the middle; some grains in this sample retained the cytological contents (Fig. 47 inset) including intine. *Pausandra densiflora* (Fig. 48) has more slender subunits with deep striations.

Ricinocarpeae, Figures 49–57

In this small tribe of five genera, *Alphandia*, *Bertya*, *Beyeria*, *Cocconerion*, and *Ricinocarpos*, the pollen of some species could be interpreted as derived—both muri and subunits are modified and or difficult to delimit. *Beyeria leschenaultii* (Fig.

54) appears to have lost definable muri—the subunits rest on a trace of footlayer over a thin lamellate endexine; however, no Crotonoideae pollen examined in TEM has hollow supratectal subunits, and if the areas marked by small arrowheads (Fig. 54) are closed up, muri of a sort, supported by thick paired columellae, would be present. *Bertya gummifera* (Fig. 57) has shallow muri with paired columellae. In *Alphandia furfuracea* (Fig. 49) and *B. gummifera* (Fig. 56), some adjacent subunits have fused together. In *Ricinocarpos bowmannii* (Fig. 51), the subunits are small striate spines limited to the junctions of the widely spaced muri, and most of the surface area of the exine consists of lumina with free columellae; however, two other species, *R. glaucus* (Fig. 50) and *R. stylosus* (Fig. 55), have a more conventional Croton structure.

The two species examined in thin section, *Beyeria leschenaultii* (Fig. 54) and *Bertya gummifera* (Fig. 57), show a very thin, sparsely granular footlayer and a thin lamellate endexine.

In LM and in TEM, the exine of *Bertya* has breaks in the footlayer/endexine where the upper ektexine appears to "unravel" outward (Fig. 57, top right), forming a pouchlike protrusion, giving the appearance of pores.

Crotoneae, Figures 58–66

Of the 13 species of *Croton* examined, *C. matourensis* (Figs. 58, 59) is the most distinctive: clavaelike supratectal elements occur only at the junctions of the widely spaced but thick muri (see legends of Figs. 58, 59). In this species, almost all of the acetolyzed pollen wall is lumina consisting of small granules above and below a thread of exine. The mostly radial section of *C. draco* (Fig. 63) reflects the morphology depicted in SEM (Fig. 62)—large subunits and lumina with fine granules. Most of the *Croton* species examined here (Table 1) have subunits that are striate or ridged to some extent, and one of the more distinctive is *C. floribundus* (Fig. 61) with umbrellalike subunits; even tangential sections, e.g., *C. texensis* (Fig. 65), show furrows. Clearly, the diversity of supratectal size, distribution, and striation reflects the large number of species in *Croton*.

Joannesieae, Figures 67–72

The two species examined in this small tribe, *Joannesia princeps* (Figs. 67–69) and *Annesijoa novoguineensis* (Figs. 70–72), have well-defined muri and, for Crotonoideae, thick columellae. In the latter species, the subunits (Fig. 70) have attenuate tips and prominent furrows/ridges; the footlayer (barely visible in Fig. 72) appears to consist of a thin layer of tiny granules, and is subtended by a thin but recognizable endexine in both tangential (Fig. 71) and radial sections (Fig. 72). The grain in Figure 72 is only partially acetolyzed and the clear layer (delimited by open arrowheads) is the remains of intine. The footlayer/endexine in Figure 69 of *Joannesia* appears nonexistent, but in other thin sections is present as a sparsely and loosely granular zone.

Aleuritideae, Figures 73–79

In another small tribe comprising scarcely a dozen species, two species were examined in SEM and TEM. *Aleurites fordii* (Figs. 73–75) has subunits with rounded apices, thin muri, and an irregular, discontinuous footlayer/endexine. *Ricinodendron rautanenii* (Figs. 76–79) also has thin muri with a threadlike continuous footlayer/endexine. Figures 76 and 77 illustrate the variation in subunit spacing found within a collection (Table 1), but the open configuration (Fig. 77) is much more common than the denser one (Fig. 76). From the spacing of the subunits in Figure 78, this section is probably from a grain more like that in Figure 77 than in Figure 76.

Neoboutonieae, Figures 80–88

In this large tribe of 13 genera, the three species examined, *Anomalocalyx uleanus* (Figs. 80–82), *Grossera major* (Figs. 83, 84), and *Crotonogyne argentea* (Figs. 85–88), have striate subunits, well-defined muri, lumina with at least some free columellae, and a thin granular footlayer/endexine. Although the thin section of *G. major* (Fig. 83) does not include muri, they are visible in SEM (Fig. 84) and in other sections. The deep subunit striations in *C. argentea* are prominent even in TEM (Figs. 85, 88).

The pollen morphology/exine structure of the remaining four subfamilies is briefly described.

Phyllanthoideae, Oldfieldioideae, Acalyphoideae, and Euphorbioideae

Webster (1987) considered Phyllanthoideae as comprising 50 genera and 2000 species. According to Punt (1962, 1987), this subfamily has two distinct, yet related, pollen lines: one is 3-colporate, prolate, and mostly reticulate without much ornamentation; the other line is distinctly, often coarsely, reticulate, and more or less oblate. Certainly the vast majority of Phyllanthoideae pollen illustrated in LM by Köhler (1965) appear to be 3-colporate. Poole (1981), using LM, SEM, and TEM, documented the wide diversity in seven species of *Zimmermannia*. The pollen of *Fluggea*

flexuosa, examined but not illustrated here (Nowicke, unpublished data), is very similar in TEM to *Euphorbia pulcherrima* (Fig. 95), which in turn could be representative of dicotyledons in general.

Phyllanthus, however, has diverse aperture types as well as a wide array of tecta. Punt (1987: 137) described the pollen of *Phyllanthus acuminatus* as being "inaperturate and pilate, but there are more endoapertures [than in *P. orbiculatus*] and they are usually arranged at random." However, the collection examined here (Table 1) has pilate pollen (Fig. 96) but with three (ecto-) apertures, each consisting of an elongate, prominently bordered "colpus" that is joined midway between the rounded ends. These "bowtielike" apertures are placed equidistant from each other and, if my interpretation is correct, they are vertically oriented (the long axis is perpendicular to the equator of the grain). To the best of my knowledge, this aperture is unique. The collection sampled is within the range of variation of those remaining identified as *P. acuminatus*.

Most Oldfieldioideae appear to be multiaperturate, brevicolporate or porate, and zonoaperturate or pantoporate (Köhler, 1965; Punt, 1962, 1987). The pollen of *Longetia buxoides* (Figs. 92, 93) is spinulose and 6–8-zonocolporate with the colpi extremely short, not much longer than the endoaperture. Thin section (Fig. 93) reveals an exine consisting mostly of a thick tectum with short columellae. The very thin footlayer and thin nonapertural endexine are similar to many Crotonoideae, but both layers are noticeably and irregularly thickened near the colporus.

In terms of genera (110), if not species (1500) (Webster, 1987), Acalyphoideae are the largest subfamily and may well have the greatest diversity of pollen (Punt, 1962). In Galearieae, all three genera, *Galearia*, *Microdesmis*, and *Panda*, were examined in SEM and TEM by Nowicke (1984) as Pandaceae. The pollen morphology and exine structure are unremarkable and thus have limited taxonomic value. The same conclusion and interpretation would apply to three species of *Macaranga* (Table 1). One of the more unusual grains in this subfamily is that of *Dalechampia humilis* (Figs. 89–91), in which a colpus transversalis (Punt, 1962) is bordered by two very prominent costae.

Certain members of Acalyphoideae, e.g., *Acidoton nicaraguensis* (Gillespie, 1994, this issue), and certain taxa in tribe Adelieae, *Adelia triloba*, *A. vaseyi*, *A. vicinelia*, and *Leucocroton cordifolius* (G. Webster, unpublished data), appear to have a crotonoid tectum–triangular supratectal elements, but the elements are small and not always distinct from each other. The tectum in *A. triloba* does form a continuous triangular array. However, none of the above species have been examined in TEM.

Euphorbioideae have never been the subject of a detailed study in SEM and TEM, but Punt (1962, 1987) did examine representative species and characterized the pollen as being consistent in shape, ornamentation, and size. Based on the above conclusions by Punt (1962, 1987), Weber-El Ghobary (1985), and El-Ghazaly (1989), the pollen of *Euphorbia pulcherrima* (Figs. 94, 95) is representative of the subfamily and could be representative of the dicots in general: 3-colporate with a perforate tectum, an endexine that is thin in the mesocolpus but thickened beneath the apertures, well developed, even elongate, columellae, and a thin footlayer.

In a largely unpublished study of Thymelaeaceae pollen (Nowicke, Patel & Skvarla), 70 species from 39 genera were examined. These pantoporate grains, illustrated here (Figs. 97–102) in SEM and in Nowicke et al. (1985) in SEM and TEM, are remarkably similar in exine structure to Crotonoideae: triangular supratectal elements are attached to prominent thick muri with short or narrow columellae, and both footlayer and endexine are thin and/or irregular.

Discussion

Pollen data from electron microscopy support and reinforce the present concept of the Crotonoideae. As demonstrated in thin section, virtually every species examined, aperturate or inaperturate, has pollen with the Croton structure—triangular supratectal elements, called subunits, attached to a network of muri having short or irregular columellae. Inaperturate exines can be further characterized by a very thin or even threadlike footlayer/endexine.

Crotonoideae are the only large assemblage in the dicotyledons to have a preponderance of inaperturate pollen. Of the 2000 species that Webster (1987) estimated for this subfamily, at most only 300 have apertures.

Colpate apertures and a particular exine structure—granular columellae, a prominent footlayer, and well-developed endexine—reinforce the segregation of *Adenocline*, *Ditta*, *Endospermum*, *Glycydendron*, *Klaineanthus*, and *Tetrorchidium* as the tribe Adenoclineae and emphasize their close relationship to each other.

It is difficult to characterize the exine structure of the 3-colpate Micrandreae until more taxa are

investigated, especially in *Micrandra*. Of all species examined here (Table 1), only *M. siphonioides* (Figs. 1–3) clearly lacks the supratectal subunits, although they appear modified in *M. kubeorum* (Fig. 4).

Within the subfamily, the pollen data suggest that Micrandreae and Adenoclineae may be primitive, having retained not only apertures but exines with well-developed footlayers and endexines.

The Manihoteae, in which two large genera (*Manihot* (170 species) and *Cnidoscolus* (75)) account for most of the 300 aperturate Crotonoideae, have porate apertures, irregular yet elongated columellae, and a thinner (than Adenoclineae) footlayer and endexine. This characterization is based on TEM data from only two species, however, and thus should be considered as preliminary.

The pollen of *Suregada*, the only genus in Gelonieae, is pantoporate but has the threadlike footlayer/endexine characteristic of the inaperturate exines. Punt (1962) classified the two species he examined as belonging to the Manihot type (periporate, tectate, Croton-pattern), but he believed the pollen similarity between *Suregada* and *Manihot* to be accidental and the result of a parallel development. I would agree that the two genera are not closely related but my opinion is based on the distinction of their pollen as revealed in thin sections, Figure 26 versus 31 and Figure 27 versus 33. The seemingly absent supporting columellae in *Suregada* further obscure its relationships with other Crotonoideae.

Although Micrandreae, Adenoclineae, Manihoteae, and Gelonieae have apertures, they have the Croton structure and are clearly allied to inaperturate Crotonoideae.

The remaining Crotonoideae have inaperturate pollen, and all species examined in thin section have the Croton structure. Although TEMs of inaperturate pollen portray a structurally weak exine—much of the surface area is covered by lumina with a wall consisting of a threadlike footlayer/endexine (e.g., Figs. 36, 44, 59, 75, 78)—acetolysis has removed the very thick intine. As demonstrated by Thanikaimoni et al. (1984: figs. 14, 15, 25, 26, 33), the intine layer is very thick and present throughout the grain. They reported intines 2–3 μm thick in *Croton matourensis*, 1.5 μm in *Domohinea perrieri*, and 1.0 μm in *Sagotia racemosa*. In contrast to other inaperturate pollen with thick intines, e.g., *Heliconia* (Kress & Stone, 1982), *Canna* (Rowley & Skvarla, 1986), Sassafras (Stone, 1987), the Crotonoideae exine is considerably thicker. Clearly, the pollen wall of inaperturate Crotonoideae is more substantial than the TEMs illustrated here would suggest.

Inaperturate pollen is a restricted condition in the dicotyledons, and its predominance in this large subfamily and rarity in the remaining Euphorbiaceae, would support the monophyly of inaperturate tribes.

It would be difficult to characterize any one, two, or even three inaperturate tribe(s) as having either advanced or generalized pollen morphology relative to those remaining. The diversity of modifications to the subunits might suggest Crotoneae, but that diversity reflects, in part, the large number of species assigned to *Croton* (750 species, Willis, 1966). Some Ricinocarpeae show the most modification, a size reduction and loss of distinction of subunits.

The exine structure of Crotonoideae is more similar to Thymelaeaceae than to any remaining subfamily of Euphorbiaceae. In fact, the very uniformity of the pollen in Thymelaeaceae and in Crotonoideae is perplexing. Thirty-three of the 39 genera examined in Thymelaeaceae have grains like those in Figures 97–102 (Nowicke, Patel & Skvarla, unpublished data).

Cronquist (1981, 1989), while acknowledging a proposed relationship between Euphorbiaceae and Thymelaeaceae based on pollen and uniovulate loculles, assigned Thymelaeaceae to the Myrtales and Euphorbiaceae to the Euphorbiales. But however well Thymelaeaceae may fit in Myrtales on other bases, pantoporate pollen is virtually unknown in the order, as is the Croton structure.

Punt (1987: 134) stated that each of the five subfamilies recognized by Webster (1989) was "more or less characterized by a basic pollen type; the subfamily Acalyphoideae is an exception to this generalization." But it seems, at least to me, that Phyllanthoideae are also an exception.

When considering all Euphorbiaceae, the pollen data are perplexing: Oldfieldioideae, Crotonoideae, and Euphorbioideae each have a basic pollen type, but it is specialized in the first two and generalized in the third; Phyllanthoideae and Acalyphoideae have diverse pollen types. In Oldfieldioideae, the pollen is brevicolporate, spinulose with a thick tectum, slender columellae, a thin footlayer, and well-developed apertural endexine. The pollen of Crotonoideae has the Croton structure and is mostly inaperturate. The pollen of Euphorbioideae, 3-colp(or)ate and tectate perforate, appears unspecialized, at least in comparison with the other subfamilies. But unspecialized or not, pollen morphology certainly does not argue against the present concept of Euphorbioideae. Pollen morphology

suggests that these three subfamilies are natural assemblages. How then, to judge the taxonomic value of pollen diversity in Phyllanthoideae and Acalyphoideae? Probably on a generic and/or tribal level. The remarkable pollen variation within *Phyllanthus* (Punt, 1987) is difficult to explain or interpret, but there are other genera with almost as much pollen diversity, e.g., *Polygonum* (Nowicke & Skvarla, 1977).

Literature Cited

Cronquist, A. 1981. An Integrated System of Classification of Flowering Plants. Columbia Univ. Press, New York.

———. 1989. The Evolution and Classification of Flowering Plants, 2nd ed. New York Botanical Garden, Bronx, New York.

Dehgan, G. & G. Webster. 1979. Morphology and infrageneric relationships of the genus *Jatropha* (Euphorbiaceae). Univ. Calif. Publ. Bot. 74: 1–73.

El-Ghazaly, G. 1989. Pollen and orbicule morphology of some *Euphorbia* species. Grana 28: 243–259.

Erdtman, G. 1952. Pollen Morphology and Plant Taxonomy. Almqvist & Wiksell, Stockholm.

———. 1966. Pollen Morphology and Plant Taxonomy. Angiosperms. Almqvist & Wiksell, Stockholm.

Gillespie, L. J. 1994. Pollen morphology and phylogeny of the tribe Plukenetieae (Euphorbiaceae). Ann. Missouri Bot. Gard. 81: 317–348.

Köhler, E. 1965. Die Pollenmorphologie der Biovulaten Euphorbiaceae und ihre Bedeutung für die Taxonomie. Grana Palynol. 6: 26–120.

Kress, W. J. & D. E. Stone. 1982. Nature of the sporoderm in monocotyledons, with special reference to the pollen grains of *Canna* and *Heliconia*. Grana 21: 129–148.

Nowicke, J. W. 1984. A palynological study of the Pandaceae. Pollen & Spores 26: 31–42.

——— & J. J. Skvarla. 1977. Pollen morphology and the relationship of the Plumbaginaceae, Polygonaceae, and Primulaceae to the order Centrospermae. Smithsonian Contr. Bot. 37: 1–64.

———, V. Patel & J. J. Skvarla. 1985. Pollen morphology and the relationships of *Aetoxylon*, *Amyxa* and *Gonystylus* to the Thymelaeaceae. Amer. J. Bot. 72: 1106–1113.

Pax, F. & K. Hoffmann. 1931. Euphorbiaceae. Pp. 11–233 *in* A. Engler & K. Prantl (editors), Die Natürlichen Pflanzenfamilien, 2nd ed., Vol. 19c. Wilhelm Engelmann, Leipzig.

Poole, M. M. 1981. Pollen diversity in *Zimmermannia*. Kew Bull. 36: 129–138.

Punt, W. 1962. Pollen morphology of Euphorbiaceae with special reference to taxonomy. Wentia 7: 1–116.

———. 1987. A survey of pollen morphology in Euphorbiaceae with special reference to *Phyllanthus*. J. Linn. Soc., Bot. 94: 127–142.

Rowley, J. R. & J. J. Skvarla. 1986. Development of the pollen grain wall in *Canna*. Nordic J. Bot. 6: 39–65.

Stone, D. E. 1987. Developmental evidence for the convergence of *Sassafras* (Laurales) and *Heliconia* (Zingiberales) pollen. Grana 26: 179–191.

Thanikaimoni, G., C. Caratini, S. Nilsson & E. Graf-strom. 1984. Omniaperturate Euphorbiaceae pollen with striate spines. Bull. Jard. Bot. Belg. 54: 105–125.

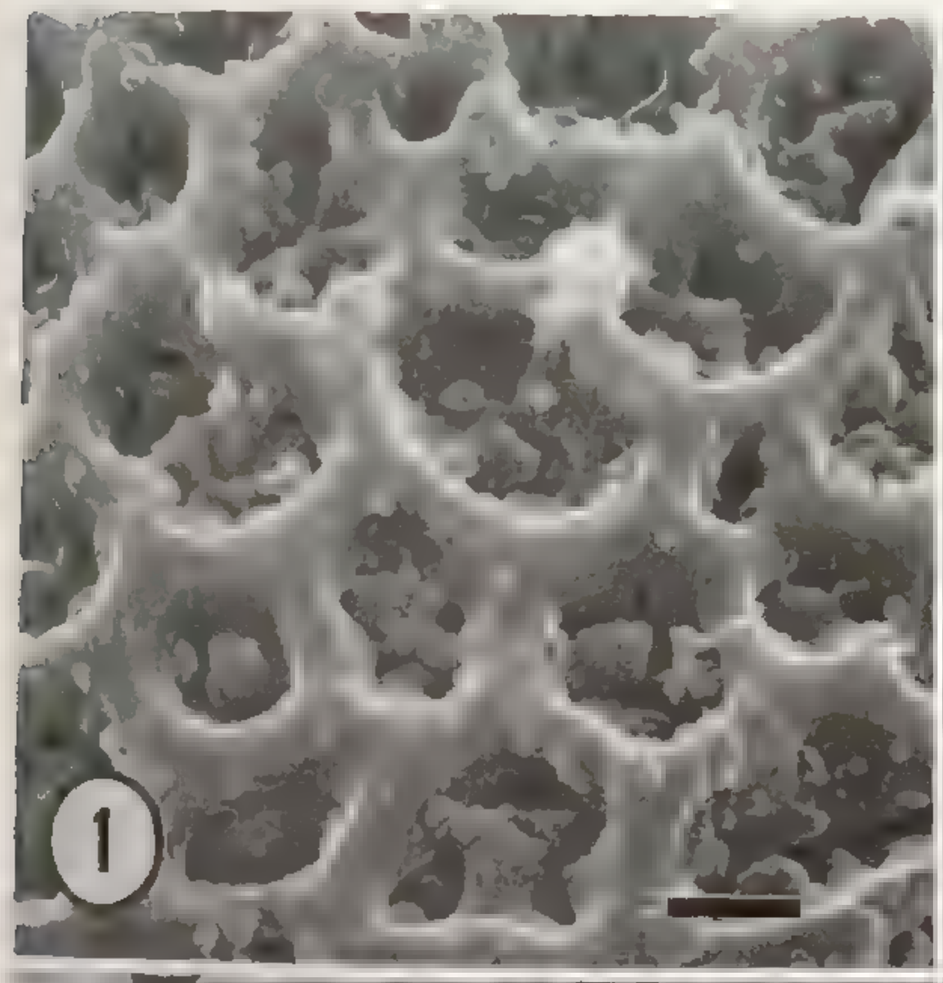
Weber-El Ghobary, M. O. 1985. Pollen morphology of four succulent species of *Euphorbia* (Euphorbiaceae). Anales Asoc. Palin. Lengua Esp. 2: 75–86.

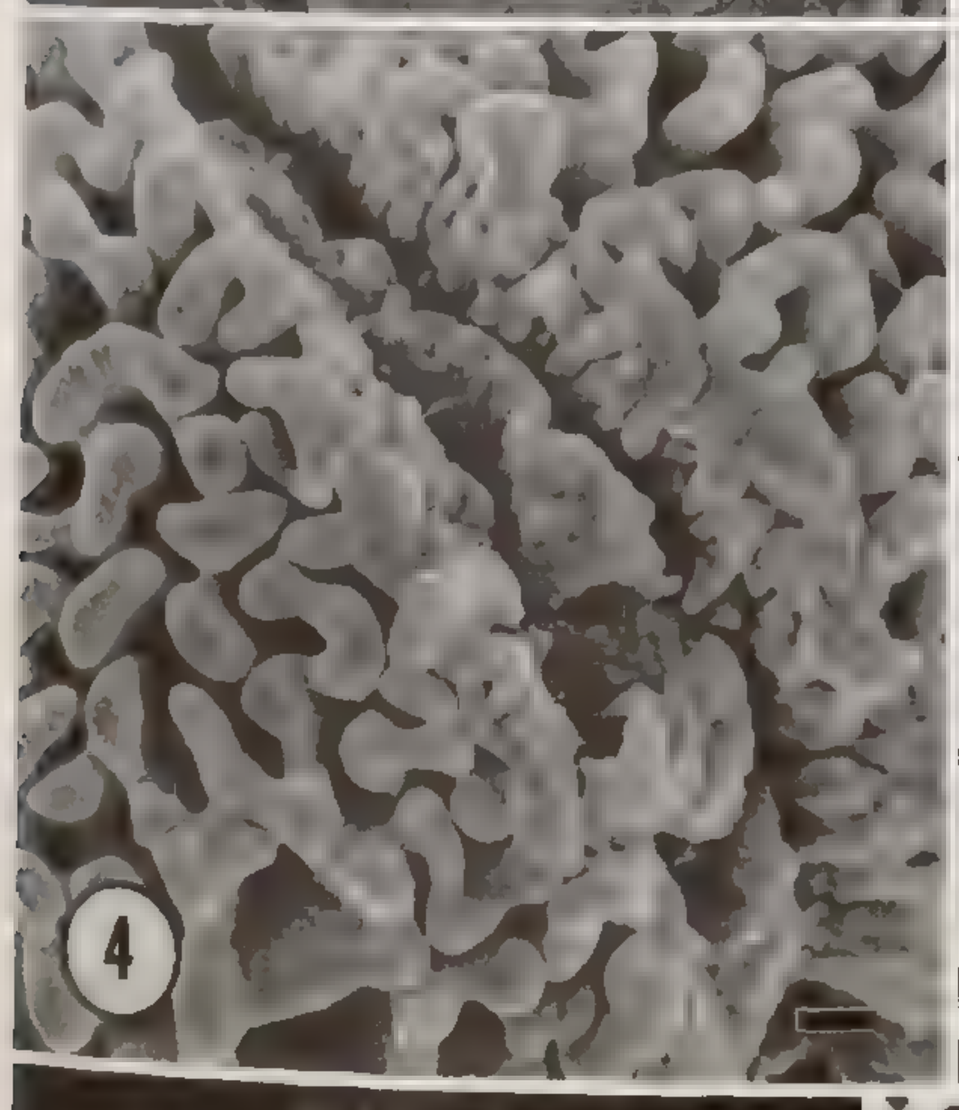
Webster, G. L. 1975. Conspectus of a new classification of the Euphorbiaceae. Taxon 24: 593–601.

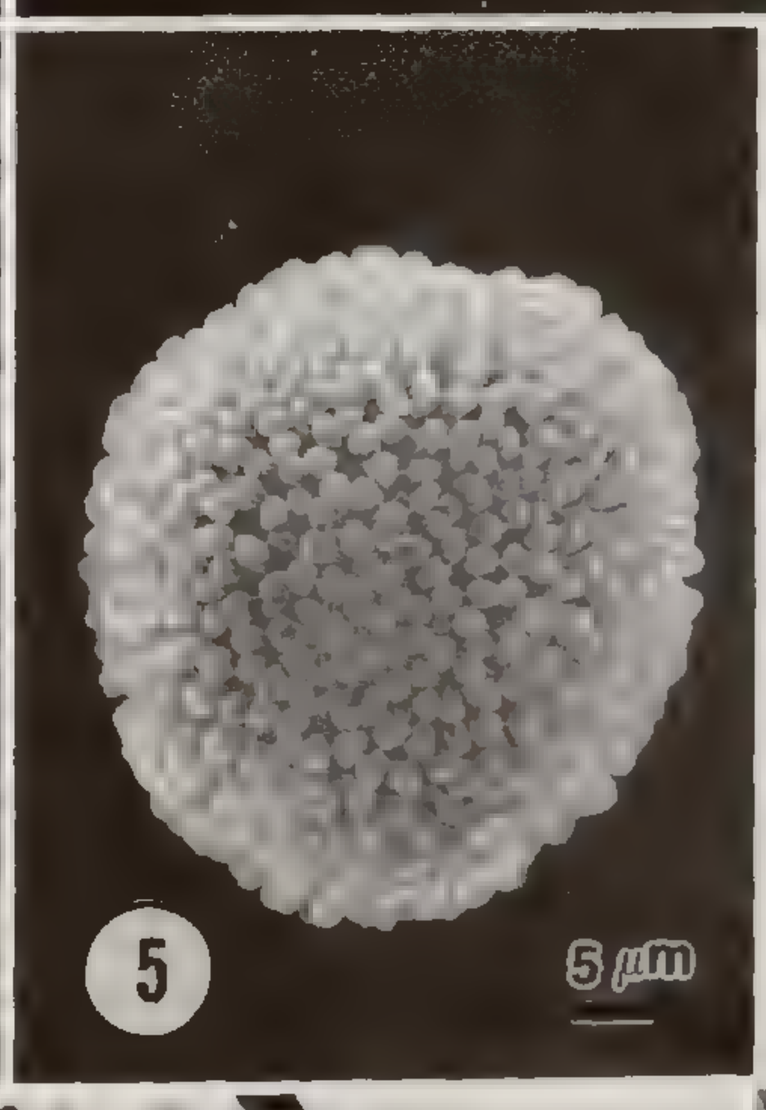
———. 1987. The saga of the spurges: A review of classification and relationships in the Euphorbiales. J. Linn. Soc., Bot. 94: 3–46.

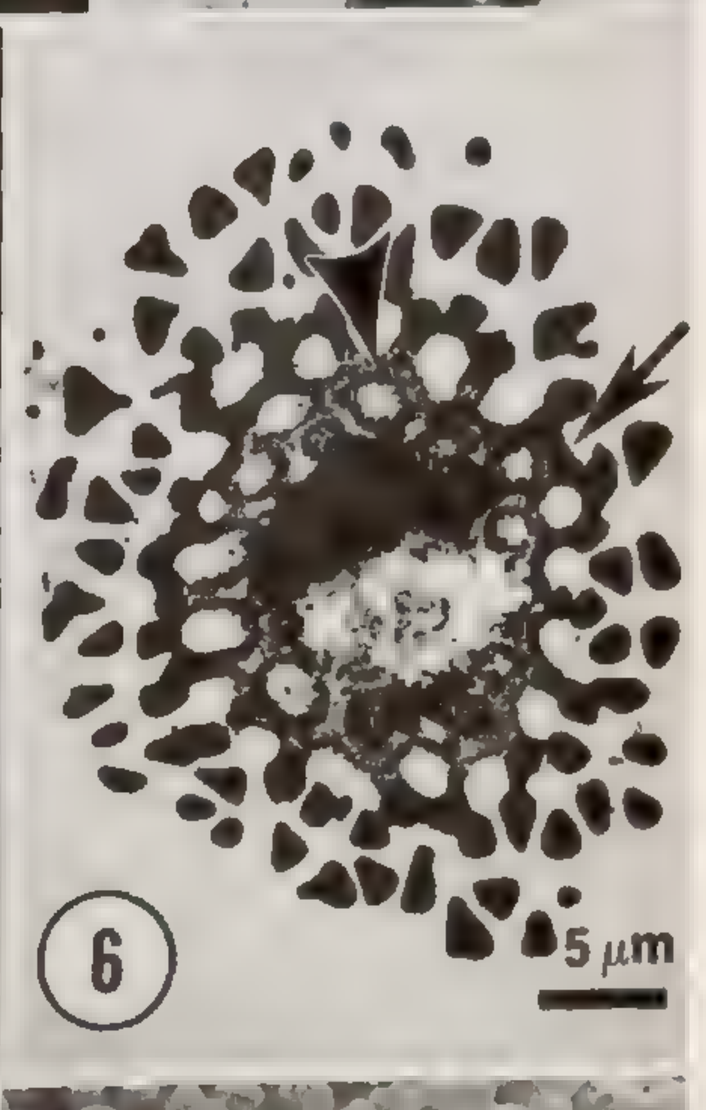
———. 1989. Revised conspectus of the Euphorbiaceae. Euphorbiaceae Newslett. 2.

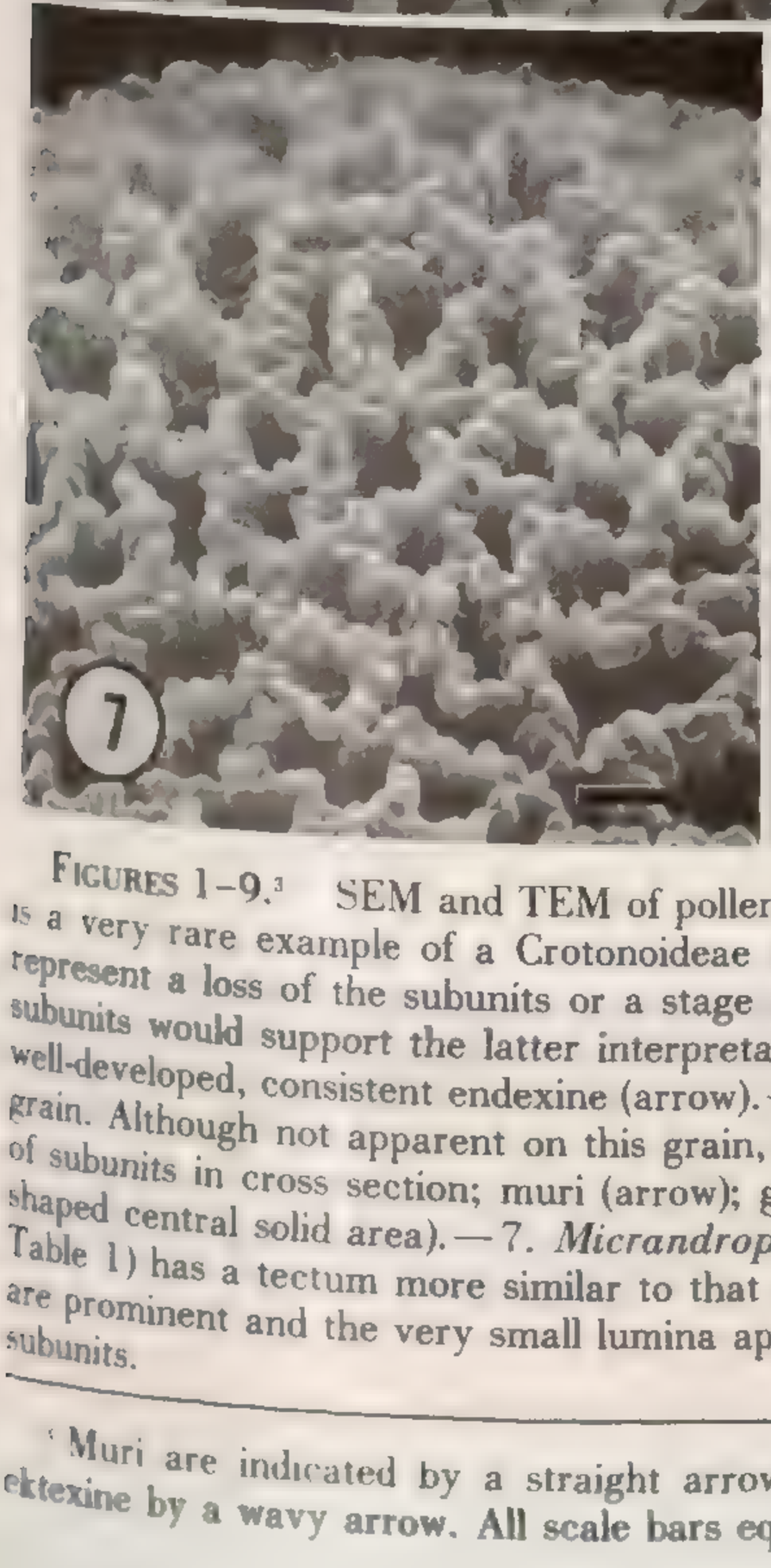
Willis, J. C. 1966. A Dictionary of the Flowering Plants and Ferns (revised by H. K. Airy Shaw), 7th ed. Univ. Press, Cambridge.

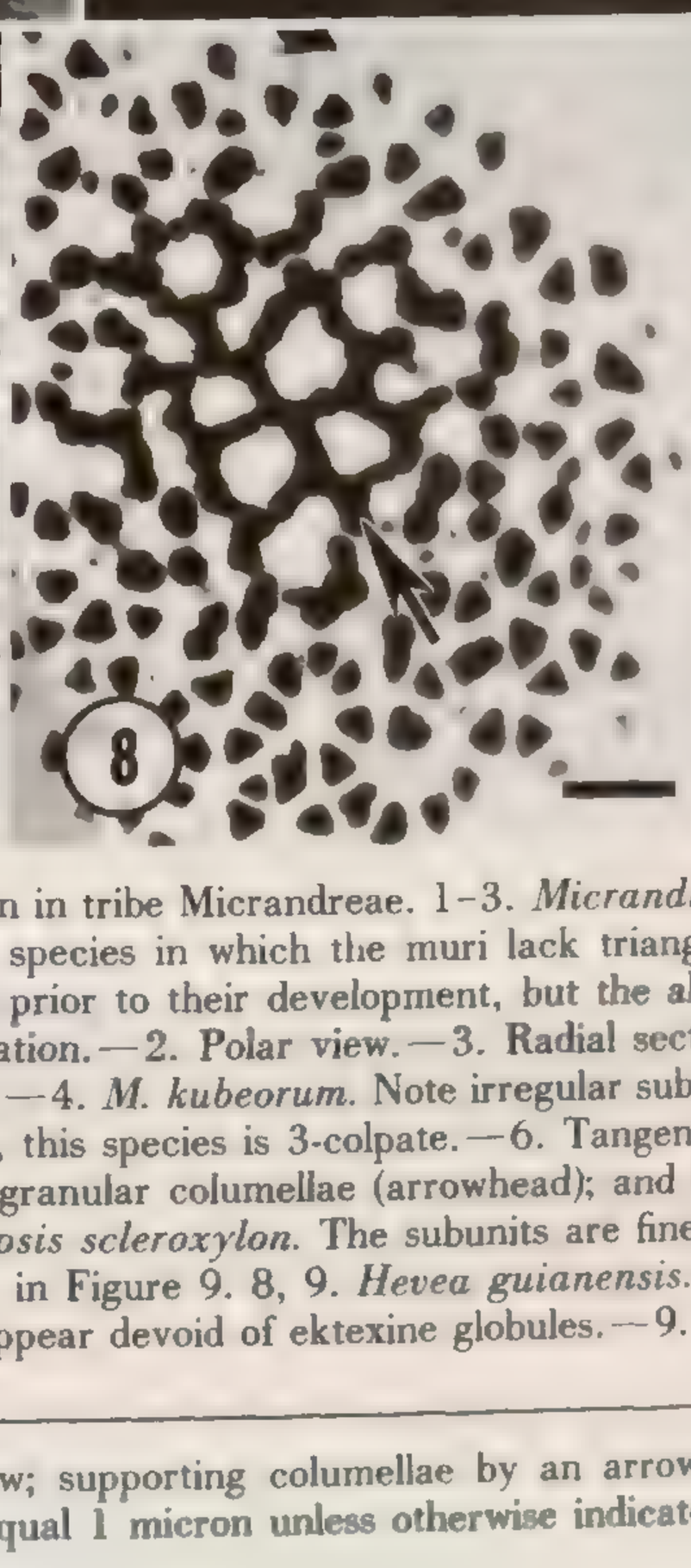


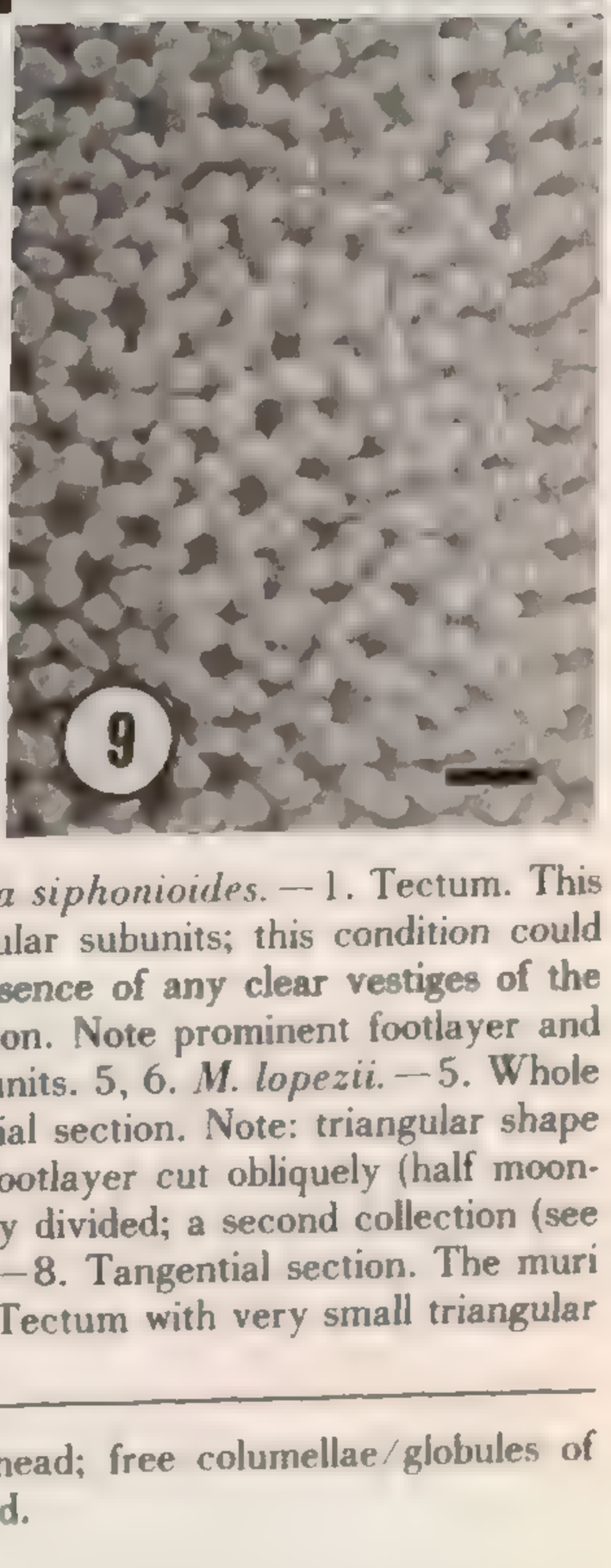






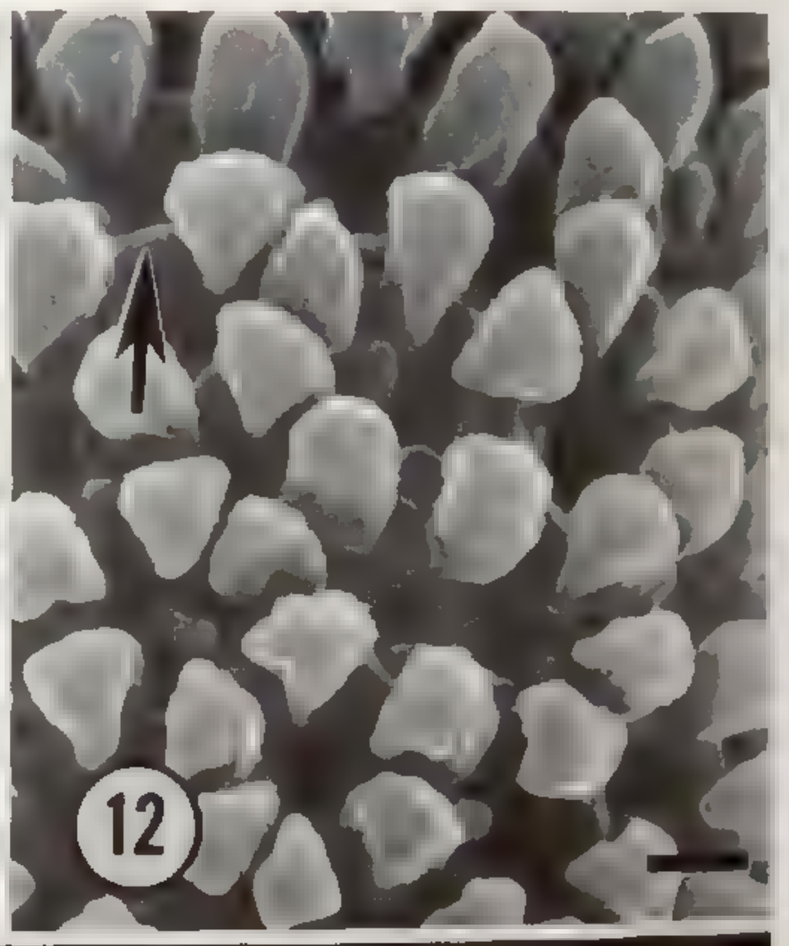


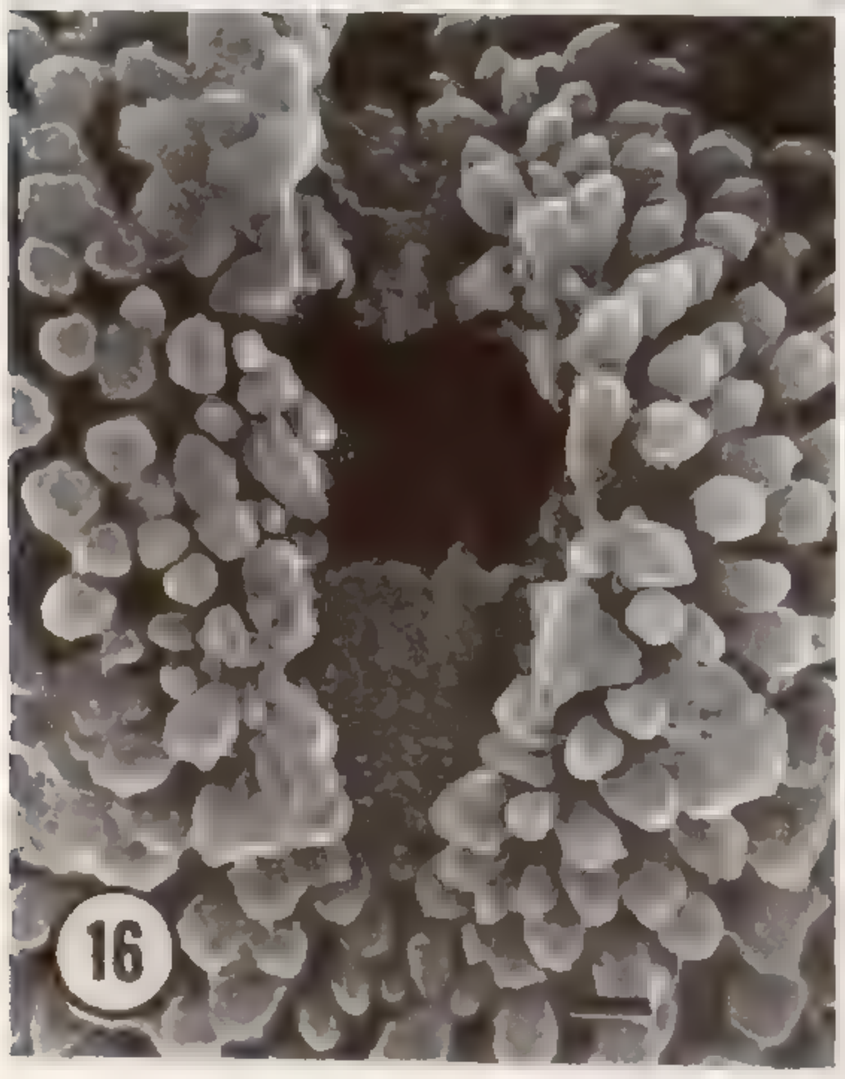


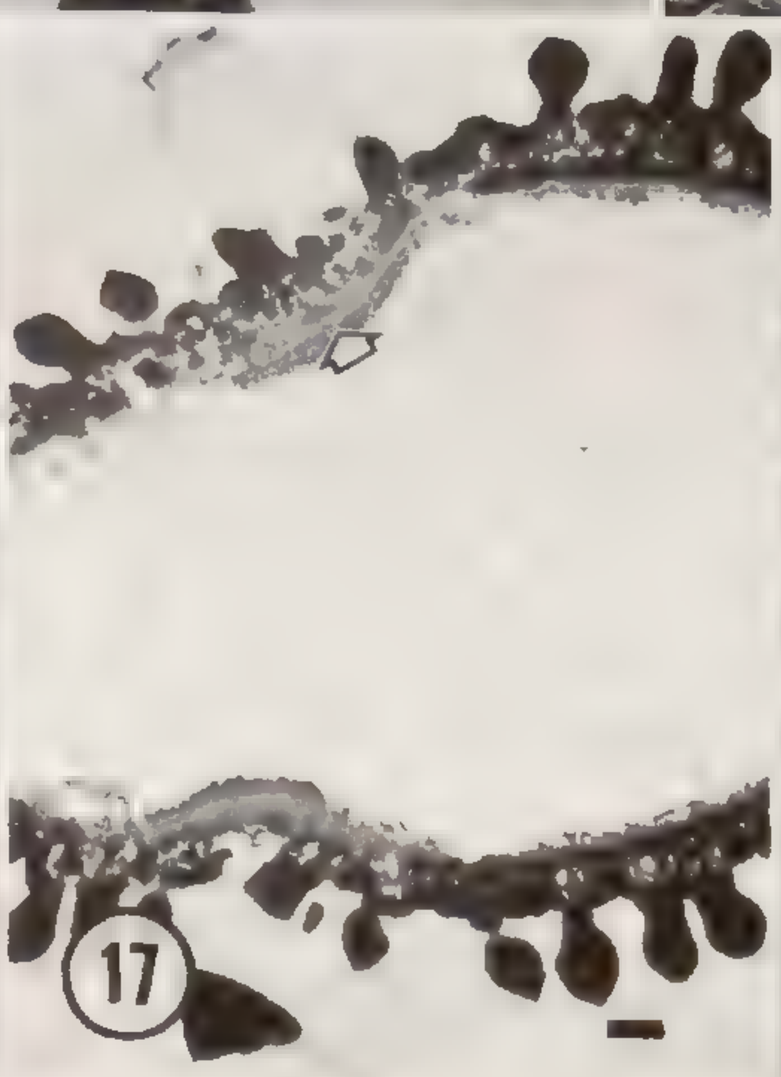


FIGURES 1–9.[3] SEM and TEM of pollen in tribe Micrandreae. 1–3. *Micrandra siphonioides*. —1. Tectum. This is a very rare example of a Crotonoideae species in which the muri lack triangular subunits; this condition could represent a loss of the subunits or a stage prior to their development, but the absence of any clear vestiges of the subunits would support the latter interpretation. —2. Polar view. —3. Radial section. Note prominent footlayer and well-developed, consistent endexine (arrow). —4. *M. kubeorum*. Note irregular subunits. 5, 6. *M. lopezii*. —5. Whole grain. Although not apparent on this grain, this species is 3-colpate. —6. Tangential section. Note: triangular shape of subunits in cross section; muri (arrow); granular columellae (arrowhead); and footlayer cut obliquely (half moon-shaped central solid area). —7. *Micrandropsis scleroxylon*. The subunits are finely divided; a second collection (see Table 1) has a tectum more similar to that in Figure 9. 8, 9. *Hevea guianensis*. —8. Tangential section. The muri are prominent and the very small lumina appear devoid of ektexine globules. —9. Tectum with very small triangular subunits.

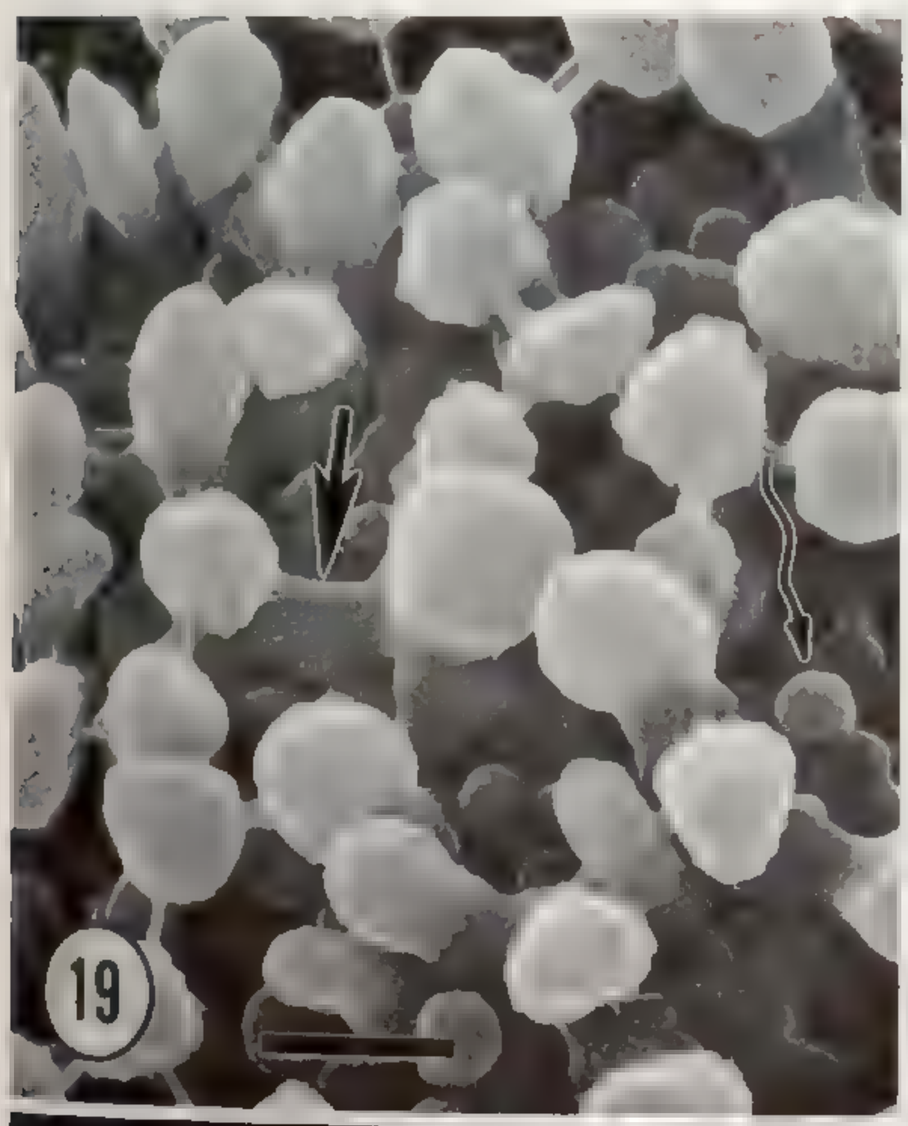
[3] Muri are indicated by a straight arrow; supporting columellae by an arrowhead; free columellae/globules of ektexine by a wavy arrow. All scale bars equal 1 micron unless otherwise indicated.

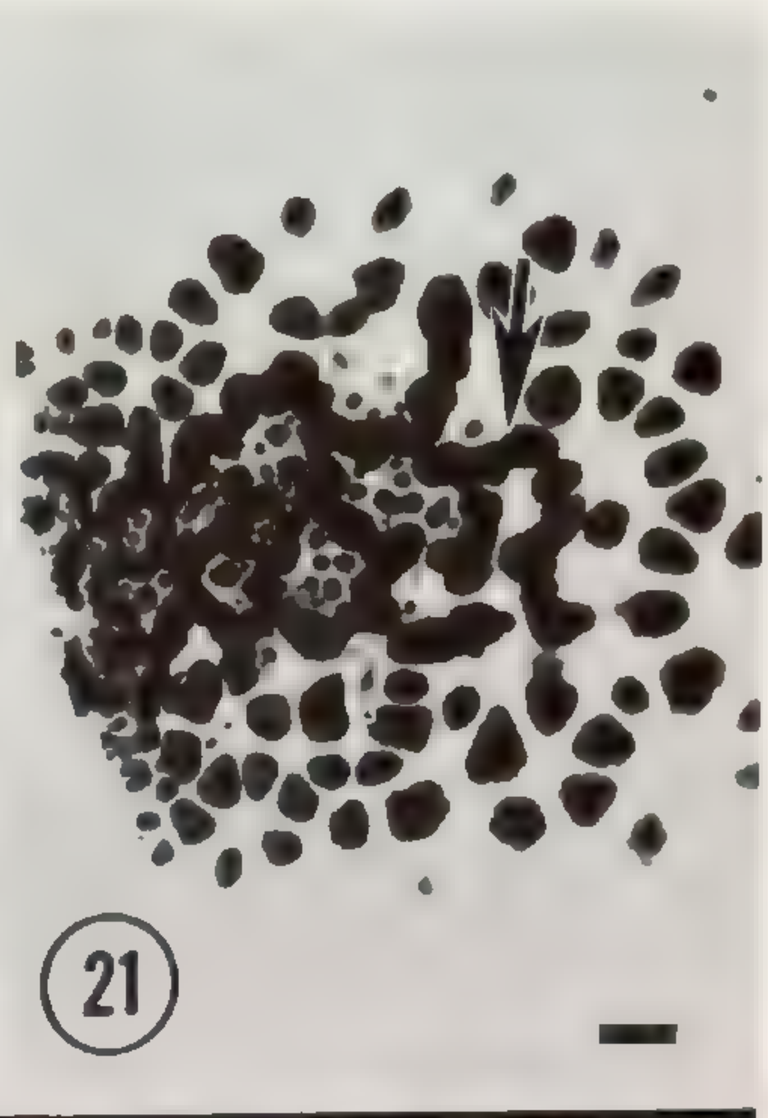


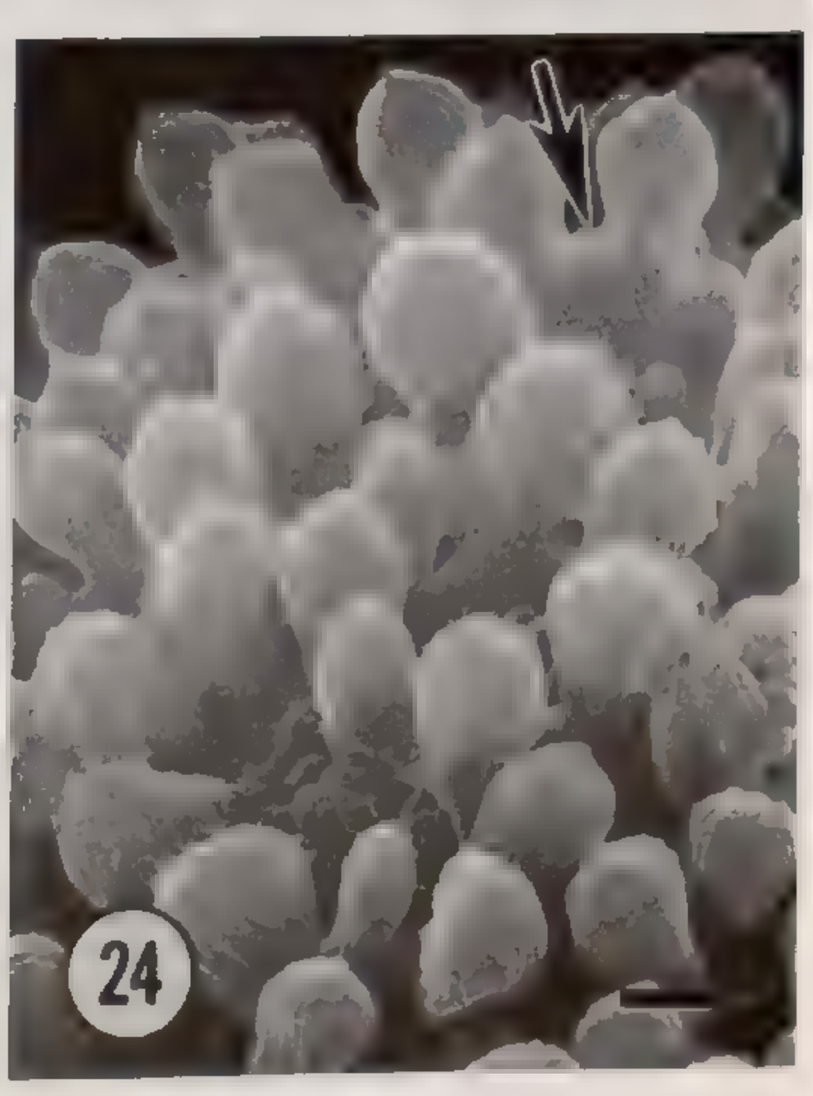




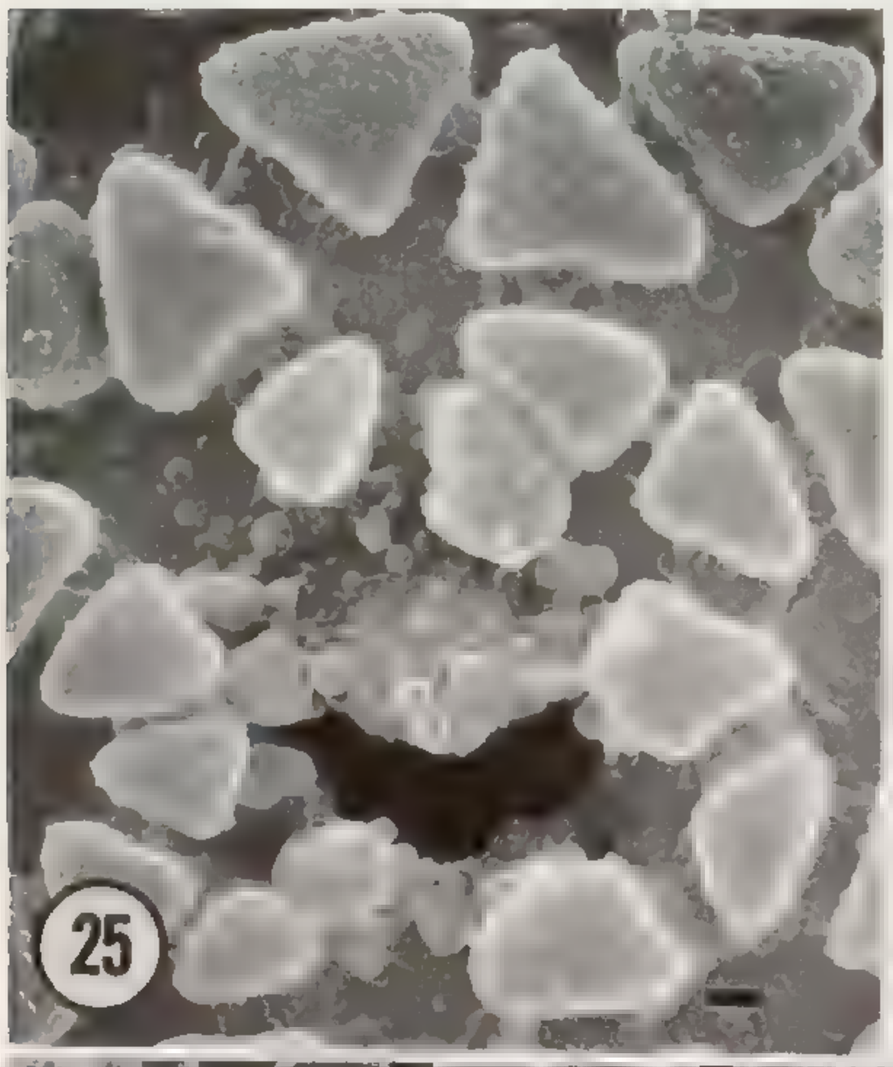
FIGURES 10–18. SEM and TEM of pollen in tribe Adenoclineae. 10–12. *Adenocline bupleuroides*. — 10. Whole grain. — 11. Oblique radial section. Note well-developed footlayer, granular columellae, and an endexine layer separating from ektexine (see also Figs. 14, 20, 23). — 12. Tectum. 13–15. *Ditta myricoides*. — 13. Tangential section. The structures, in order from the outside, are triangular subunits, then solid bars of muri, granular columellae, and solid footlayer; the seemingly absent endexine layer is assumed to be detached. — 14. Radial section. Both this species and *Tetrorchidium rubrivenium* (Fig. 20) have elongate echinate subunits that are recognizable even in LM; fl = footlayer, en = endexine. — 15. Tectum. 16, 17. *Klaineanthus gaboniae*. — 16. This was the only species examined with colporate apertures. — 17. Radial section including two apertures (arrow); although not illustrated in this grain, others had a fragmented irregular endexine similar to that in Figure 23. — 18. *Glycydendron amazonicum*. Tangential section. Structural components are same as in Figure 13. en = endexine; fl = footlayer.

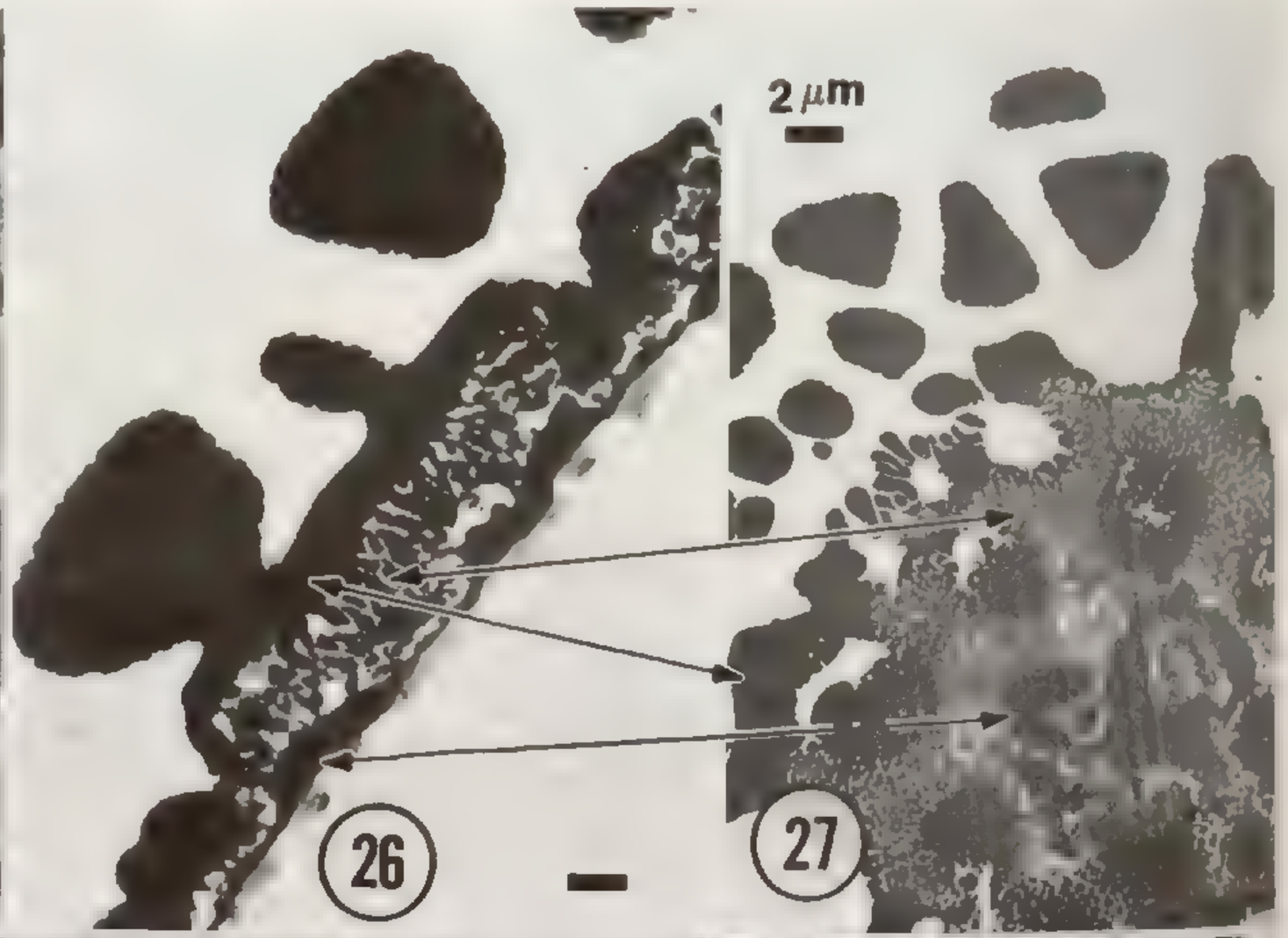


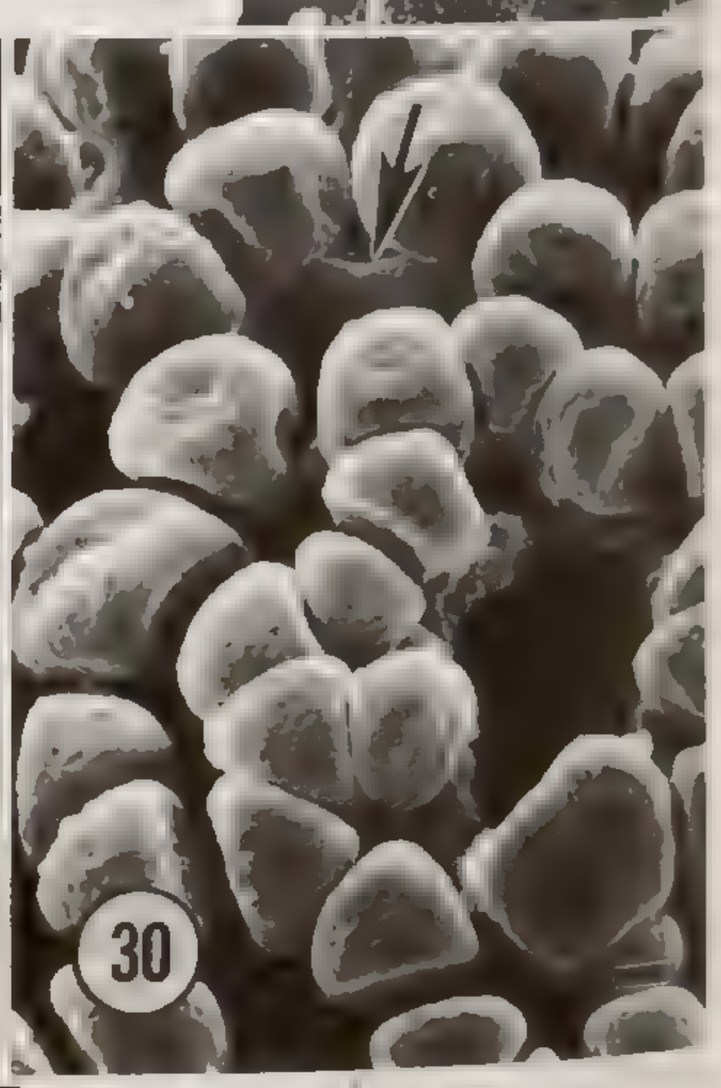


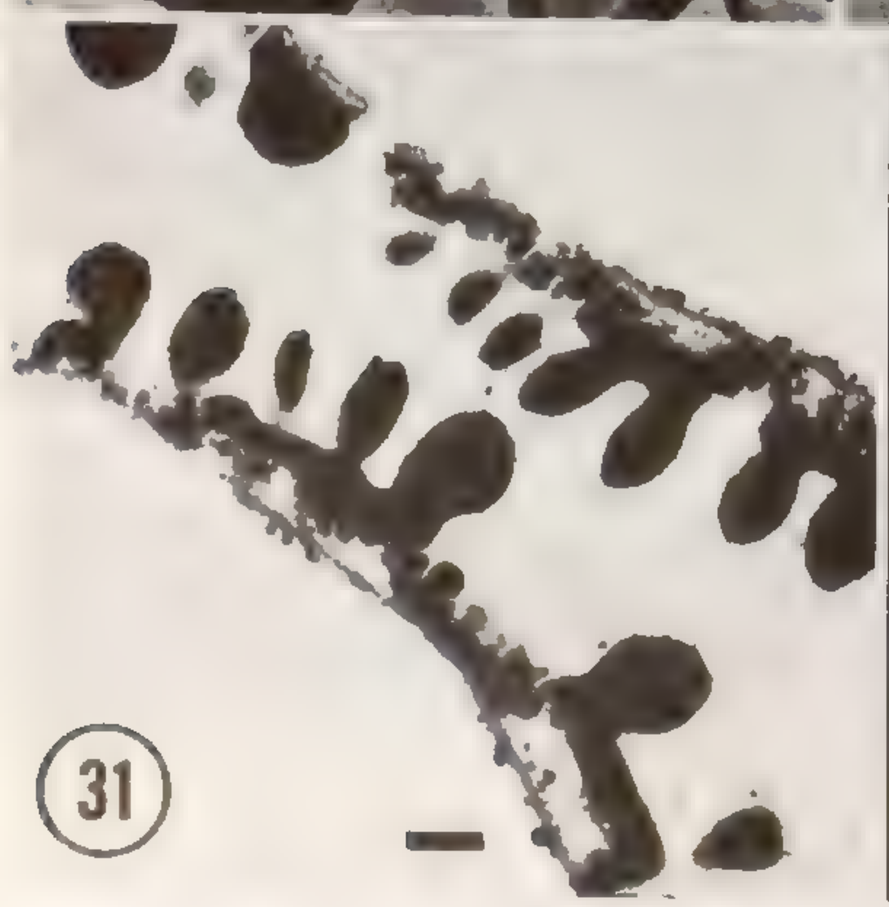


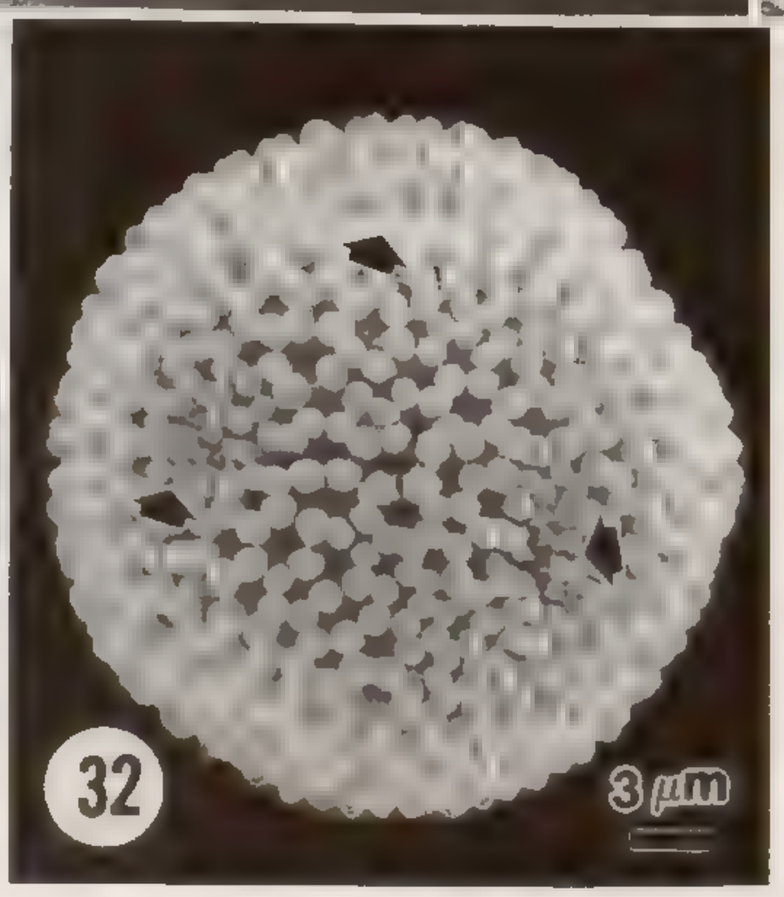
FIGURES 19-24. SEM and TEM of pollen in tribe Adenoclineae. 19-21. *Tetrorchidium rubrivenium*. —19. Tectum at high magnification. The muri are prominent, subunits are deep/long, and most lumina are covered with ektexine globules. —20. Radial section. Although muri are poorly defined, they are clearly present in Figure 19 and in the tangential section in Figure 21. —21. Tangential section. Section is too shallow to include granular columellae or footlayer. 22, 23. *Endospermum peltatum*. —22. Whole grain, polar view. A very minor portion of this sample (see Table 1) appears to have been shed as tetrads, but the tetrad-members have varying degrees of cohesion. —23. Radial section near aperture. Note: endexine layer separating from ektexine; thick irregular footlayer; granular columellae; detached endexine. —24. *E. formicarium*. Tectum with variously sized, striate subunits. en = endexine; fl = footlayer.

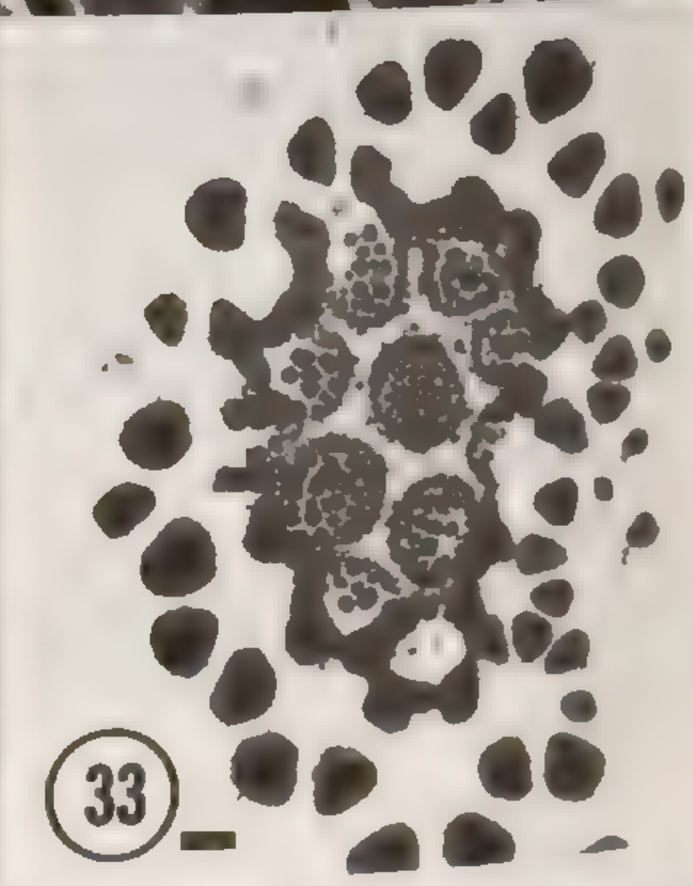




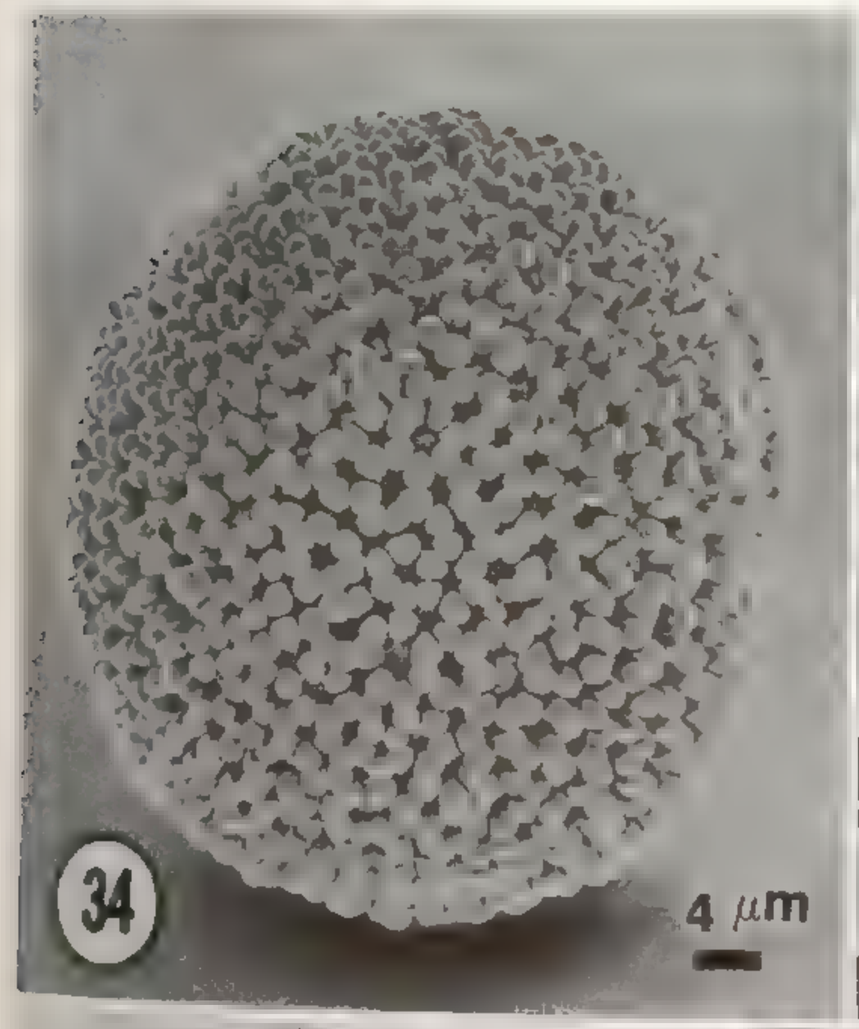


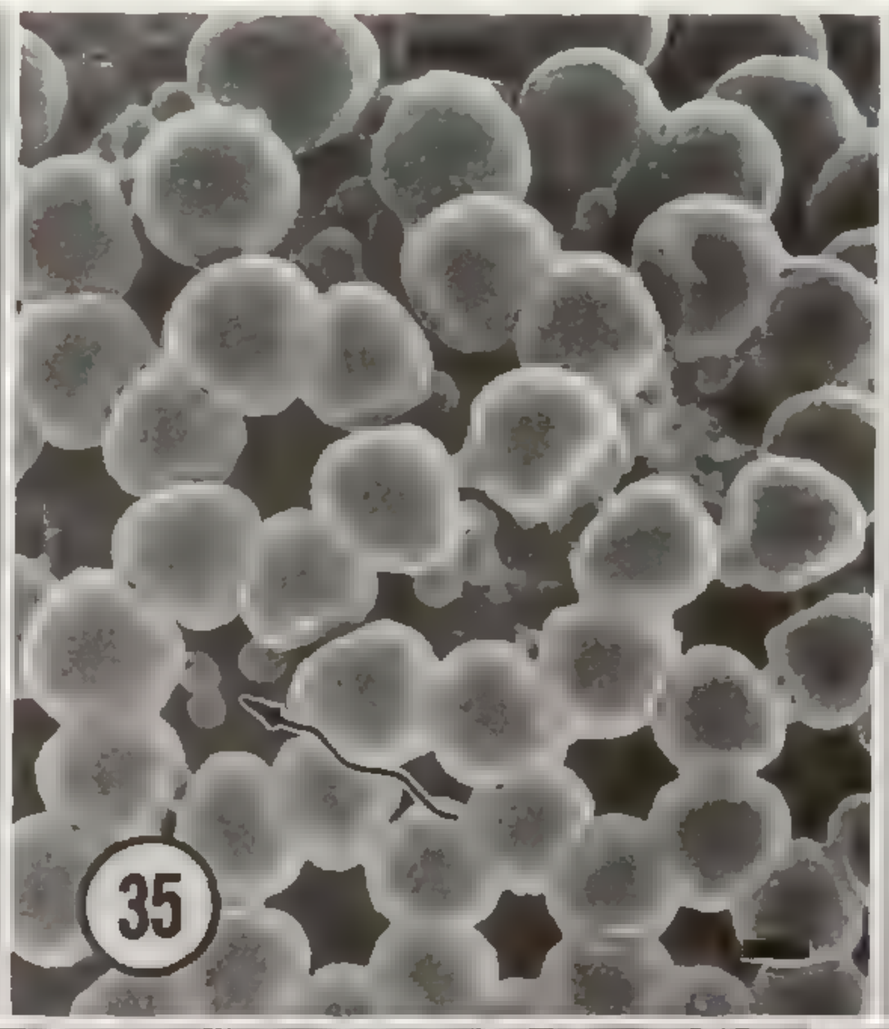


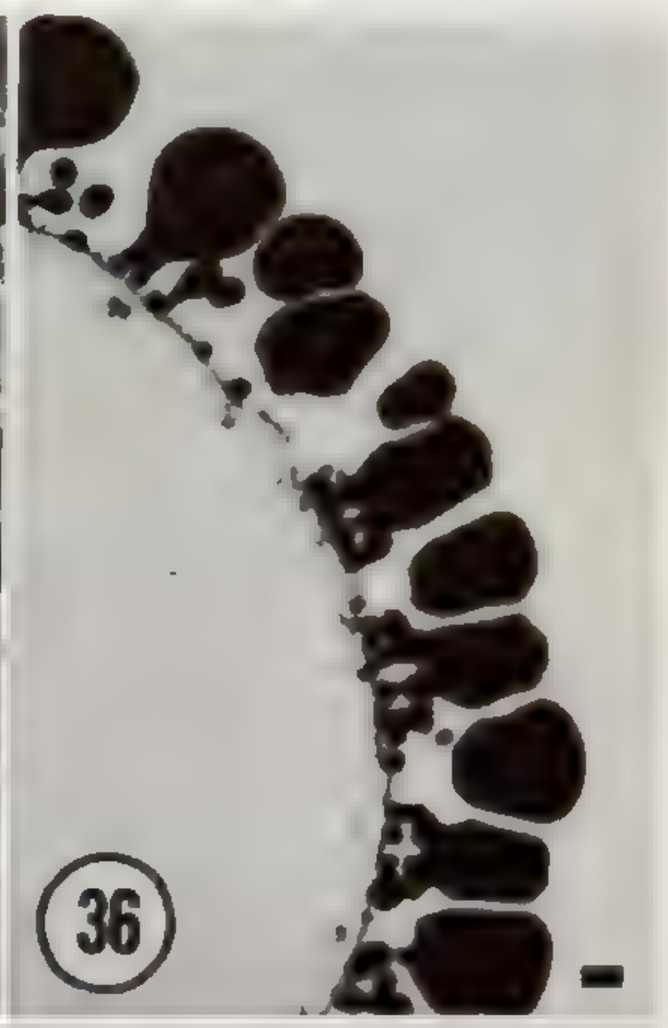


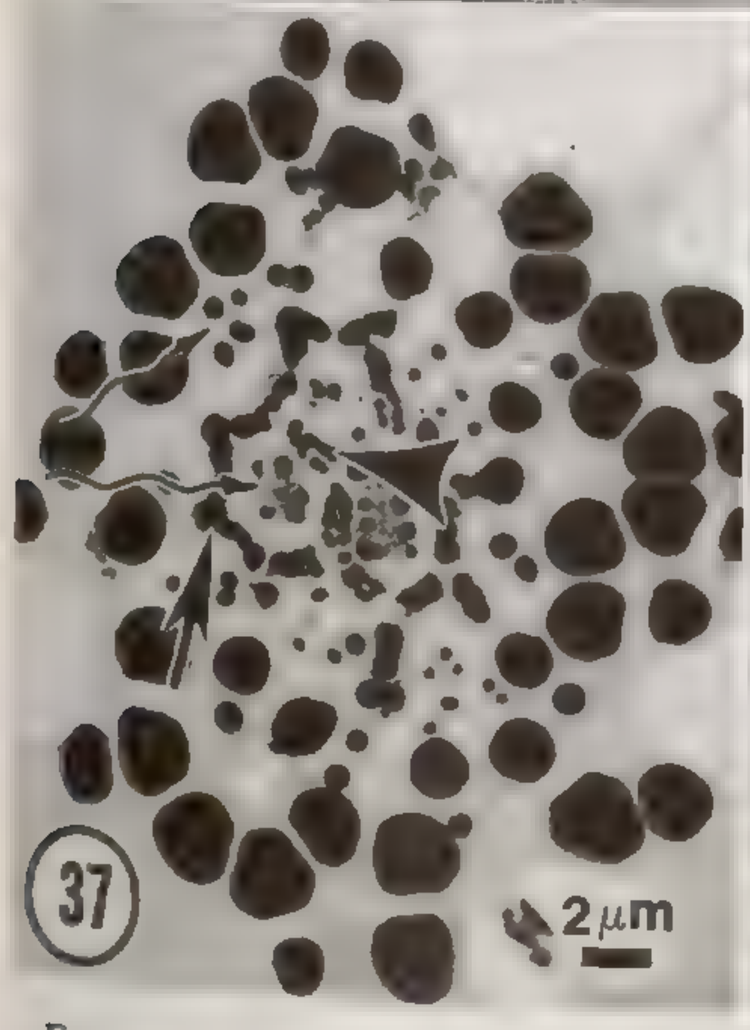


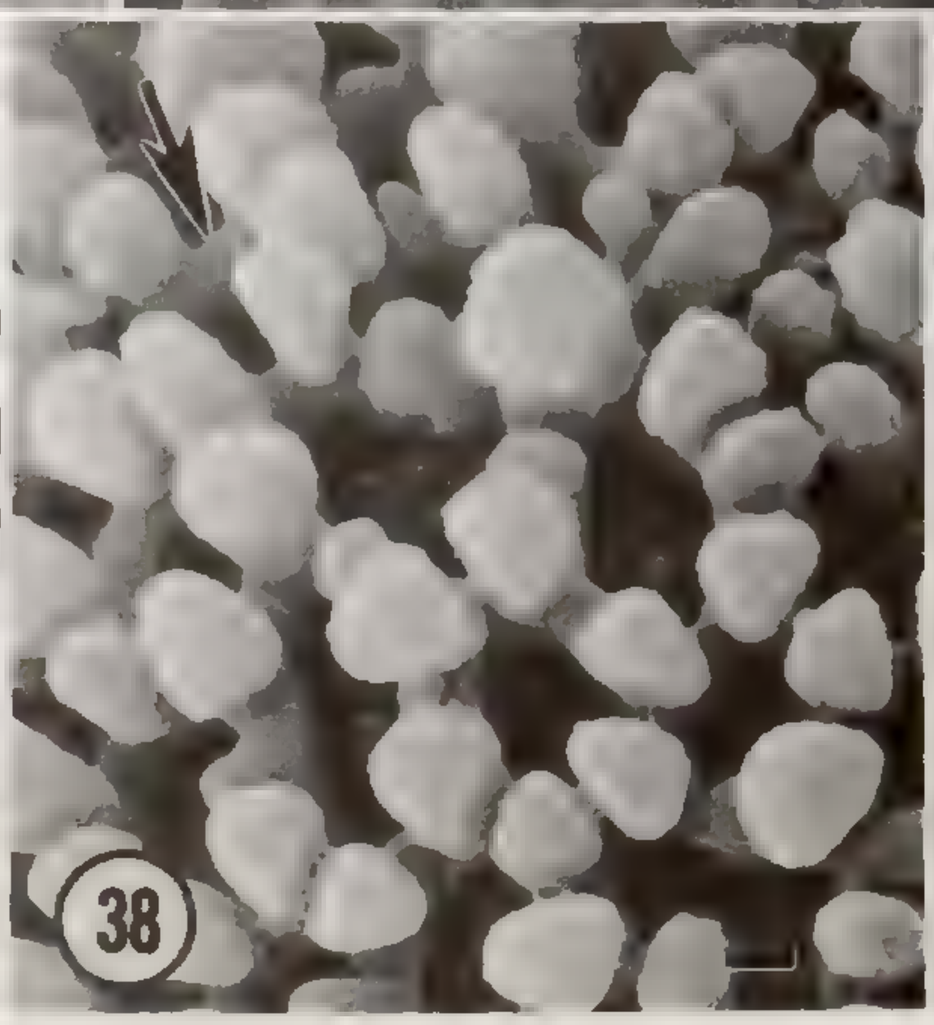
FIGURES 25–33. SEM and TEM of pollen in tribes Manihoteae (25–30) and Gelonieae (31–33). 25–27. *Manihot aesculifolia*. —25. Tectum including partially covered porate aperture; muri are inconspicuous and lumina have only sparse shallow globules of ektexine. Of all genera examined here, *Manihot* has the most consistently triangular subunits. —26. Radial section. Arrows connect (from top downward) supporting columellae, muri, and footlayer in this radial section with their counterparts in the tangential section in Figure 27; the supporting columellae are very irregular, even granular; note discontinuous but recognizable, less electron-dense endexine. —27. Tangential section. See legend of Figure 26. —28. *Manihot pilosa*. Note pitted surface of subunits, a characteristic found in many *Manihot* species examined here. —29. *Cnidoscolus rotundifolius*. Fracture illustrating relatively thick footlayer and endexine. Inset, *C. sinaloensis*. Note irregular columellae and irregular footlayer; in other sections the supporting columellae appear similar to those in Figure 26. —30. *C. sinaloensis*. Tectum with pore. —31–33. *Suregada glomerulata*. —31. Radial sections of two grains. There is a paucity of columellae below the well-developed muri; in











FIGURES 34–39.[3] SEM and TEM of pollen in tribes Jatropheae (34–37) and Elateriospermeae (38, 39).—34. *Deutzianthus tonkinensis*. 35–37. *Jatropha hastata*. —35. Tectum. The large size and dense spacing of the subunits obscures the muri; some subunits appear to be connected by thin strands of exinous material.—36. Radial section. Muri are very thin; there is an almost clear (very weakly electron-dense) endexine layer with a few granules delimiting the inner boundary.—37. Tangential section. Small circular objects between subunits, and between subunits and muri, are free columellae (see Fig. 35); note paired support columellae. 38, 39. *Elateriospermum tapos*.—38. Tectum with conspicuous muri and large lumina.—39. Radial section. The gradual thinning (left) of the well-developed footlayer suggests a preformed aperture (as opposed to a break). However, apertures could not be verified in LM.

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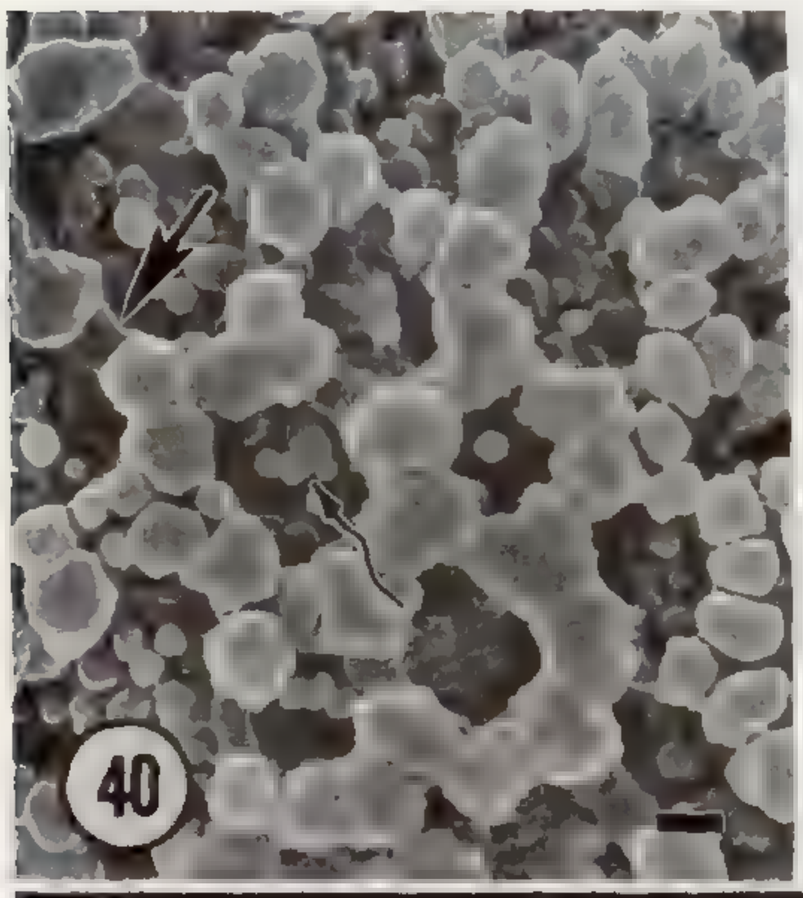
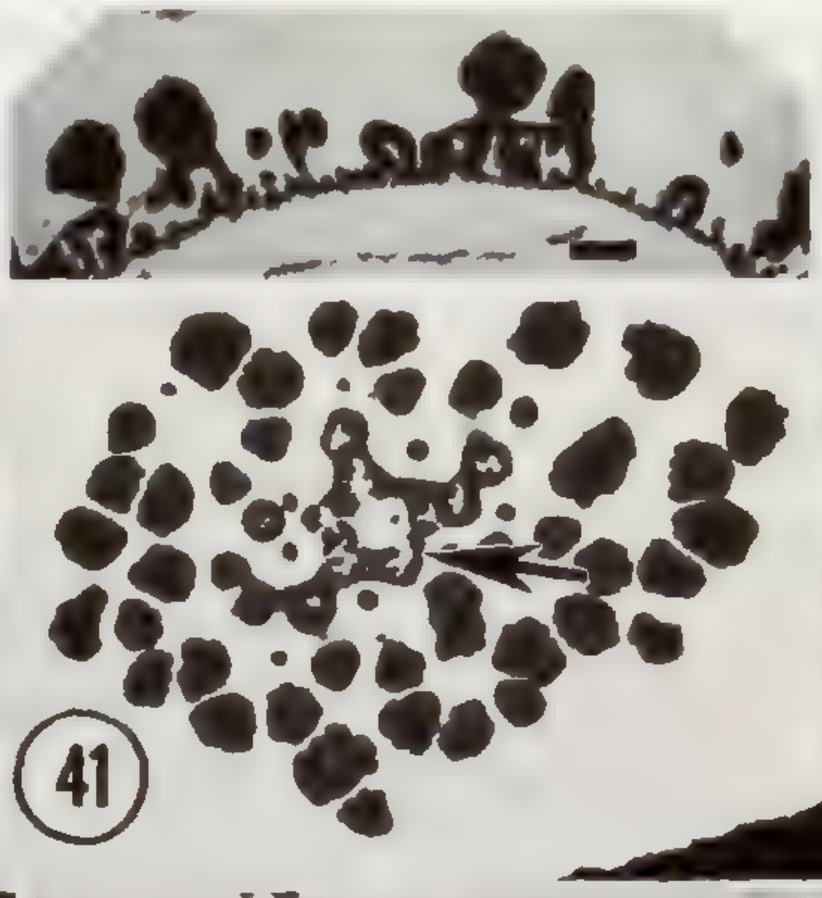
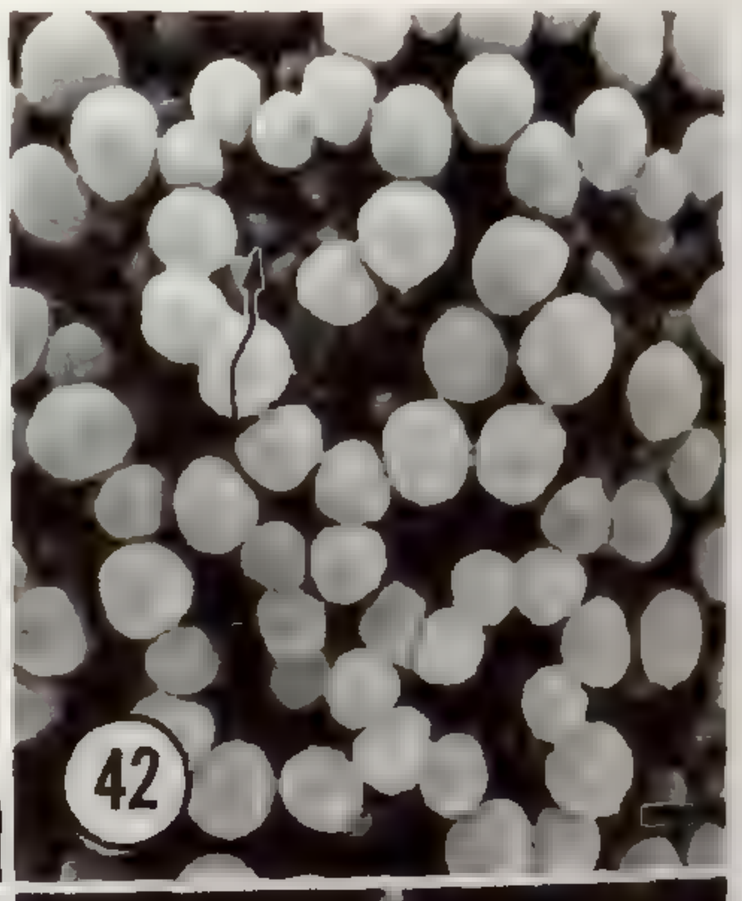
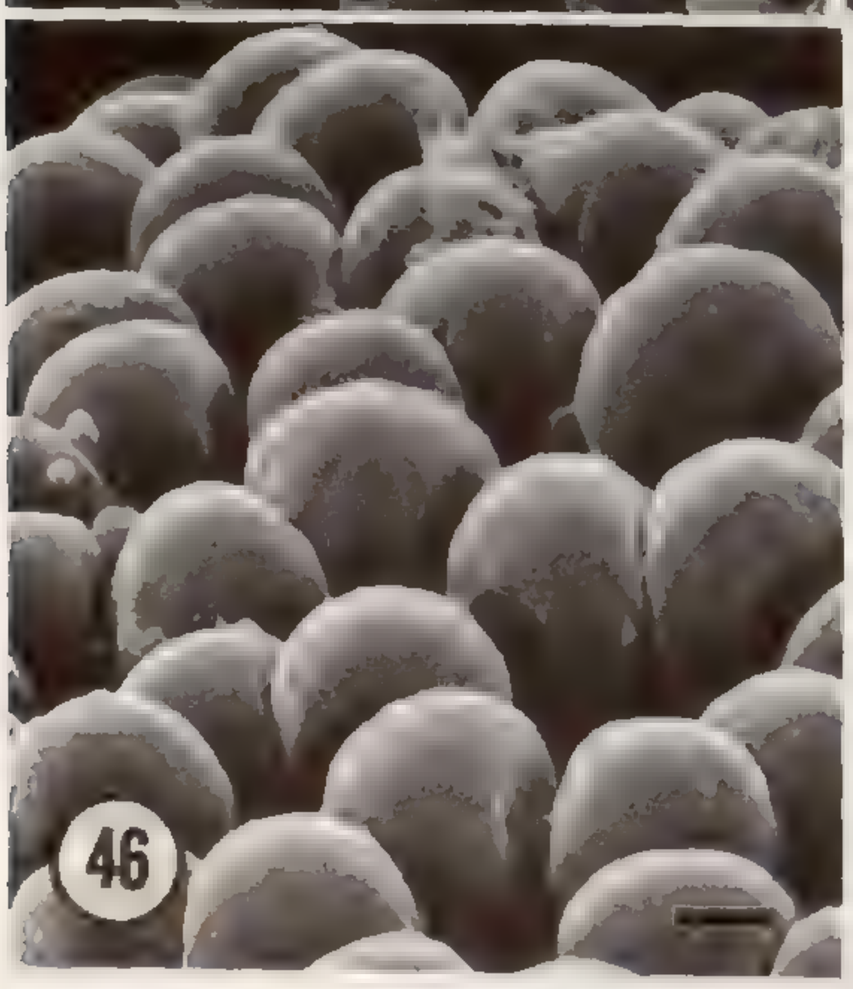
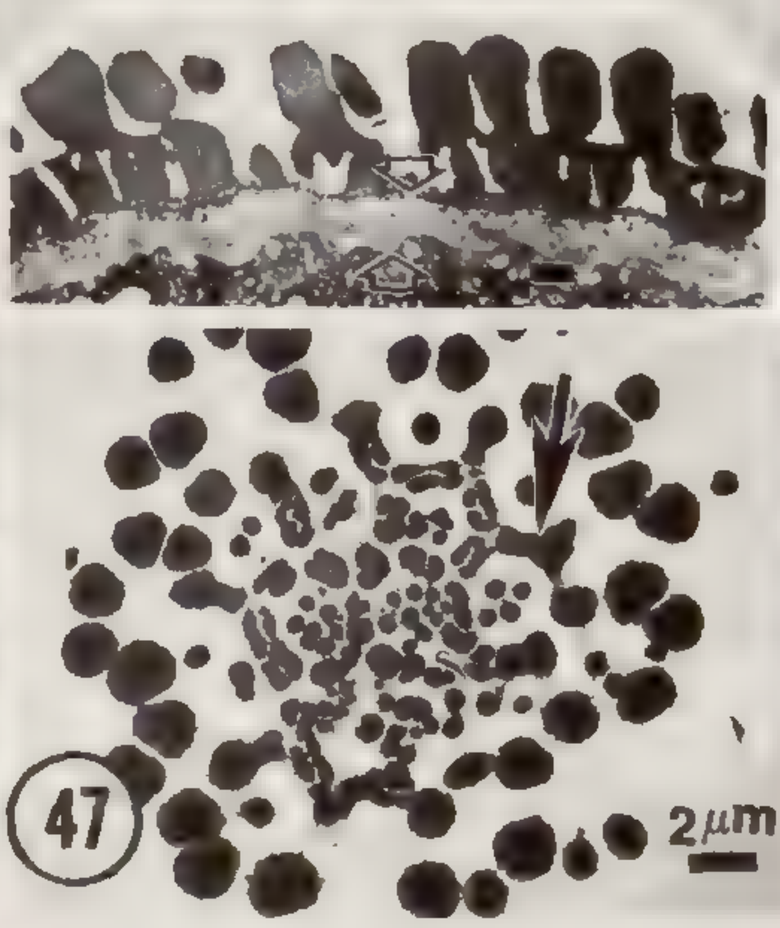
both grains the footlayer/endexine consists of small, occasional granules above and below a thread of exine; in upper grain, the size reduction of subunits indicates proximity to an aperture, but even here the endexine is threadlike.—32. Whole grain with at least three depressions (small arrowheads) indicating apertures; in high-magnification SEMs, the lumina are covered with shallow, free columellae/globules of ektexine.—33. Tangential section.



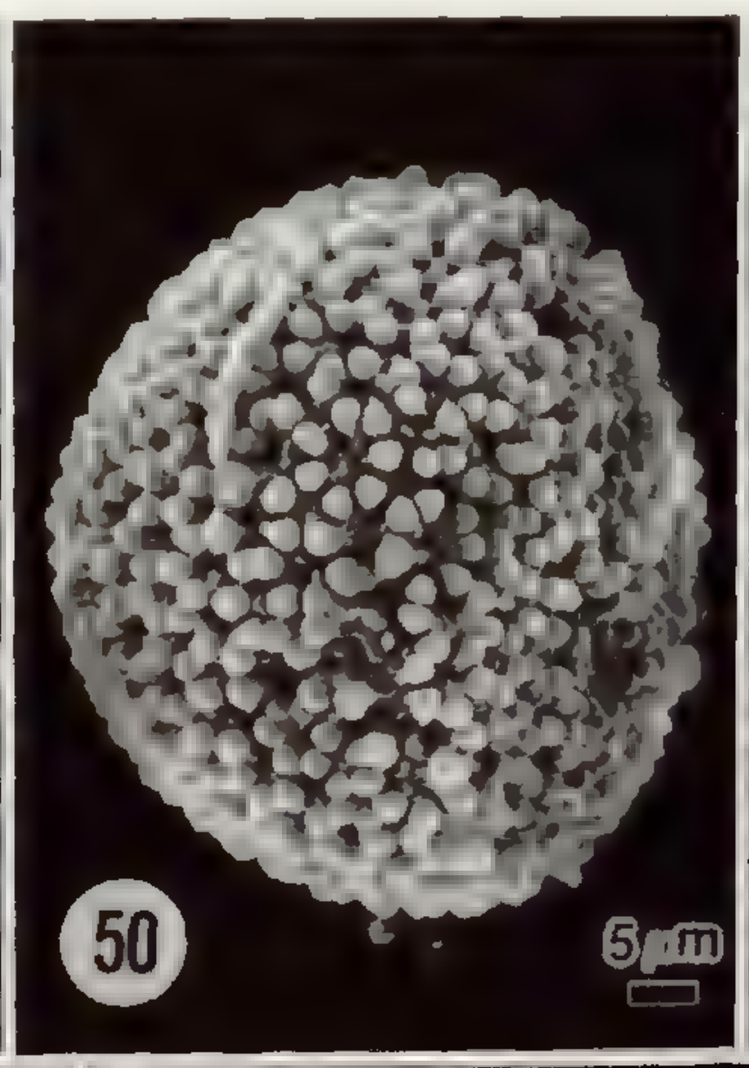


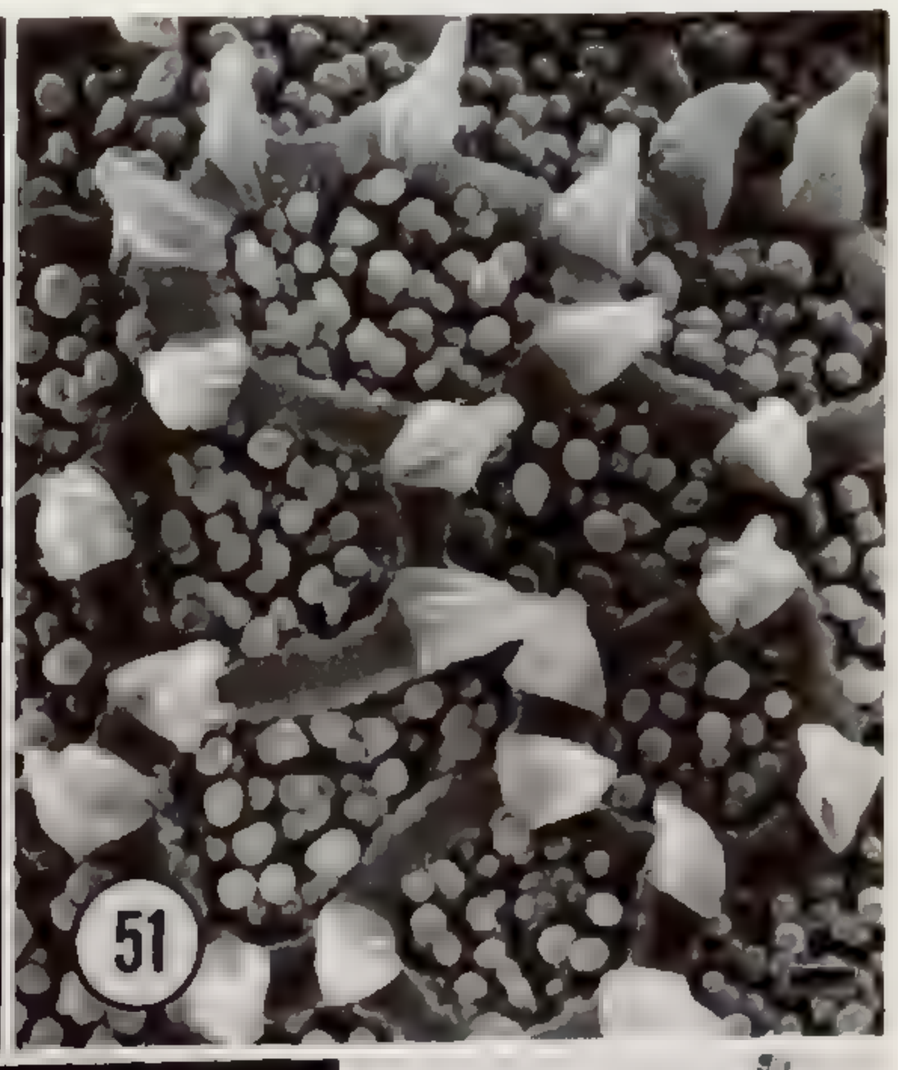


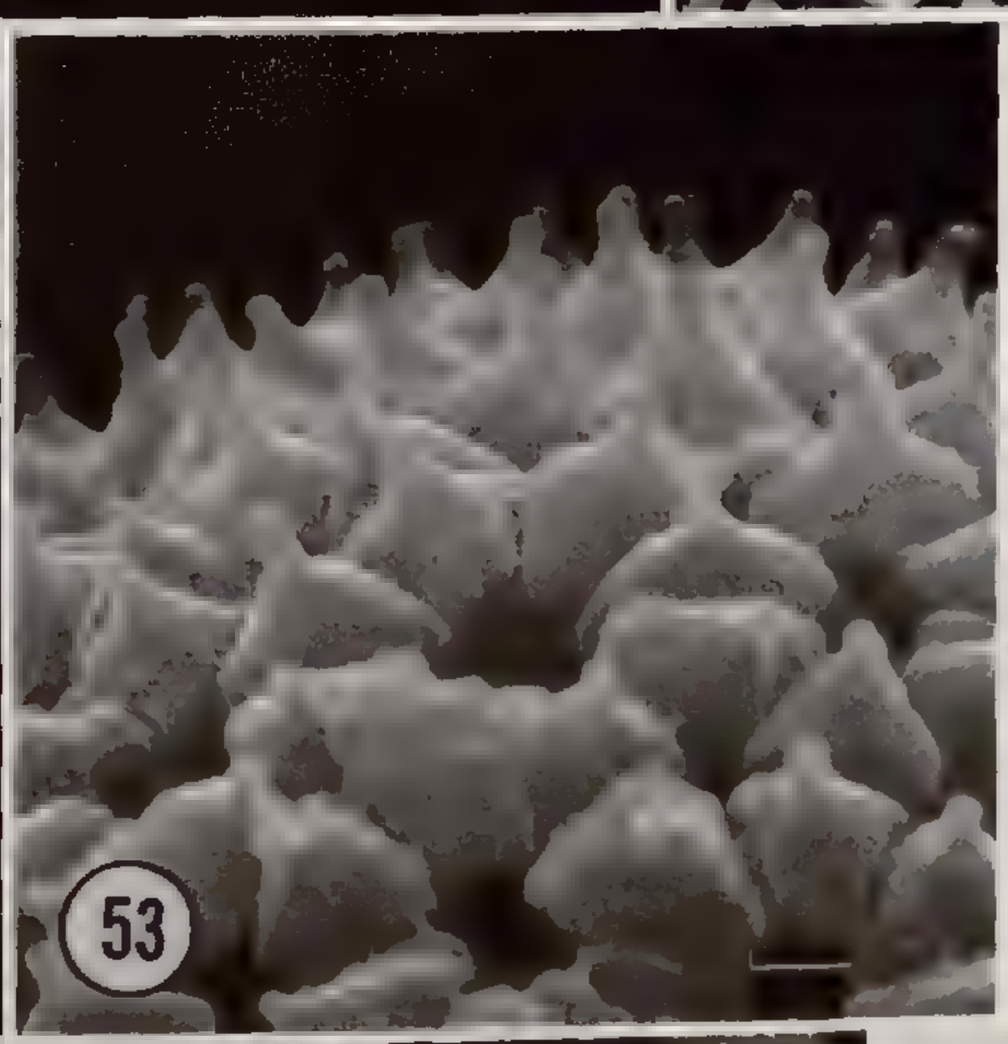


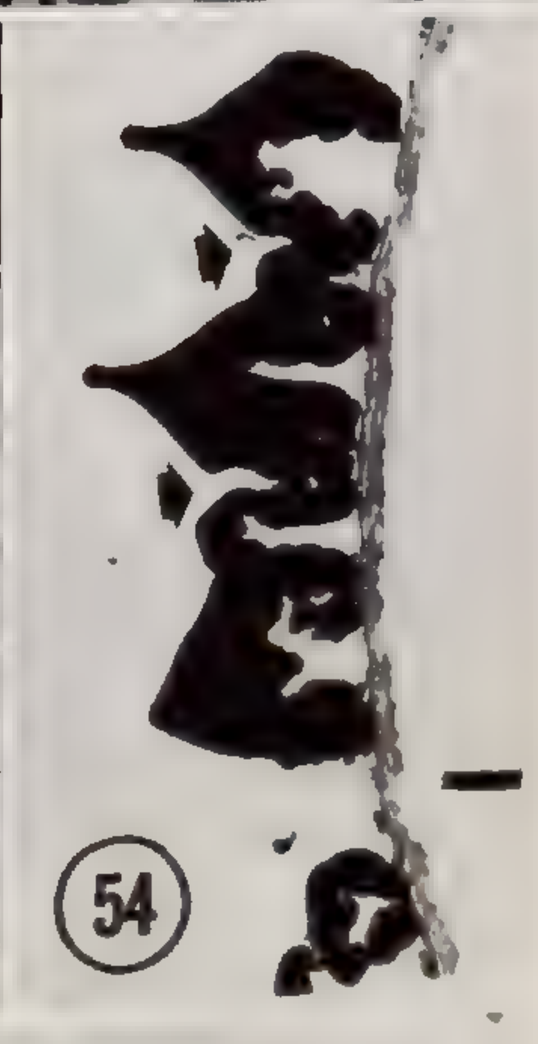


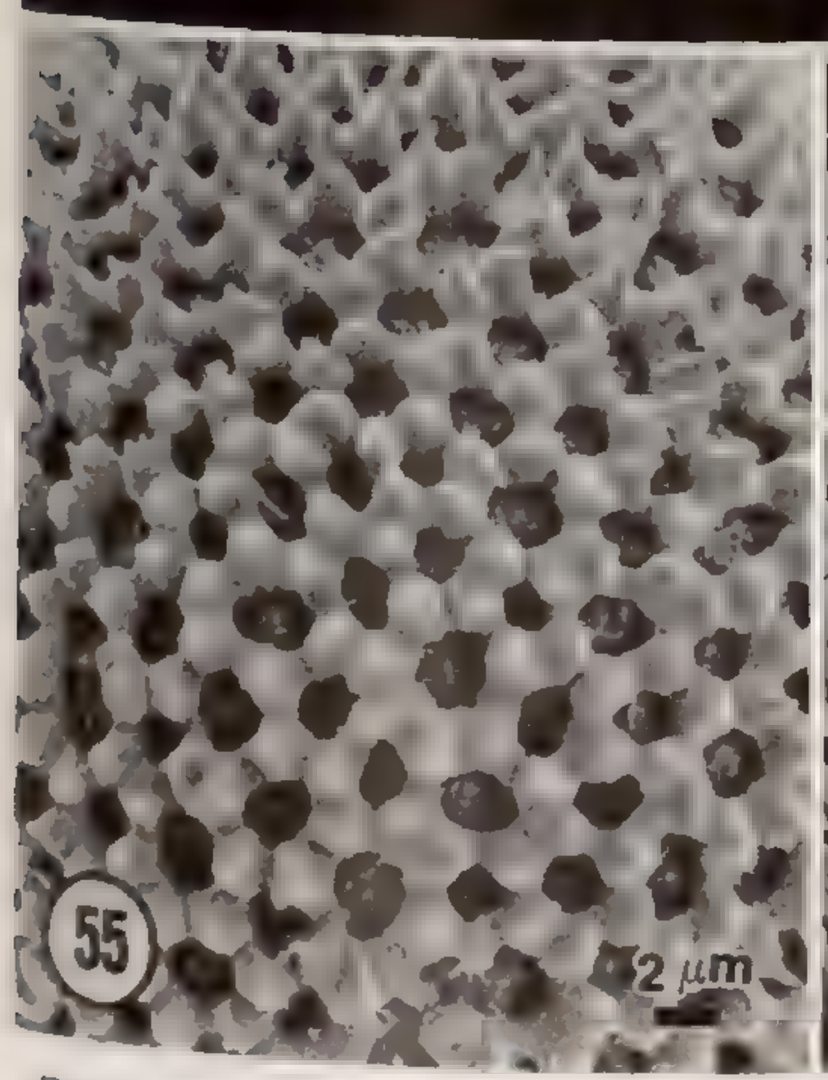
FIGURES 40–48.—SEM and TEM of pollen in tribe Codiaeae. 40, 41. *Codiaeum variegatum*.—40. Tectum with open configuration, irregularly shaped subunits, and lumina with free columellae or ektexine globules.—41. Tangential section. Inset, radial section.—42. *Pantadenia adenanthera*. Tectum with irregular muri and large lumina. 43, 44. *Sagotia racemosa*.—43. Tectum. This is one of the more distinct tecta in the subfamily; in some grains there are areas where the subunits fuse together. A similar tectum is present in *Annesijoa novoguineensis* (Fig. 70).—44. Oblique section. This section emphasizes the unusual footlayer/endexine—granules above and below a thread of exine.—45. *Dimorphocalyx luzoniensis*. 46, 47. *Ostodes zeylanica*.—46. Tectum. Although subunits are densely spaced here, other grains had a more open configuration; note faint furrows in subunits.—47. Tangential section. Inset: radial section of portion of incompletely acetolyzed grain; area between open arrowheads is intine.—48. *Pausandra densiflora*. Supratectal subunits are deeply striate.

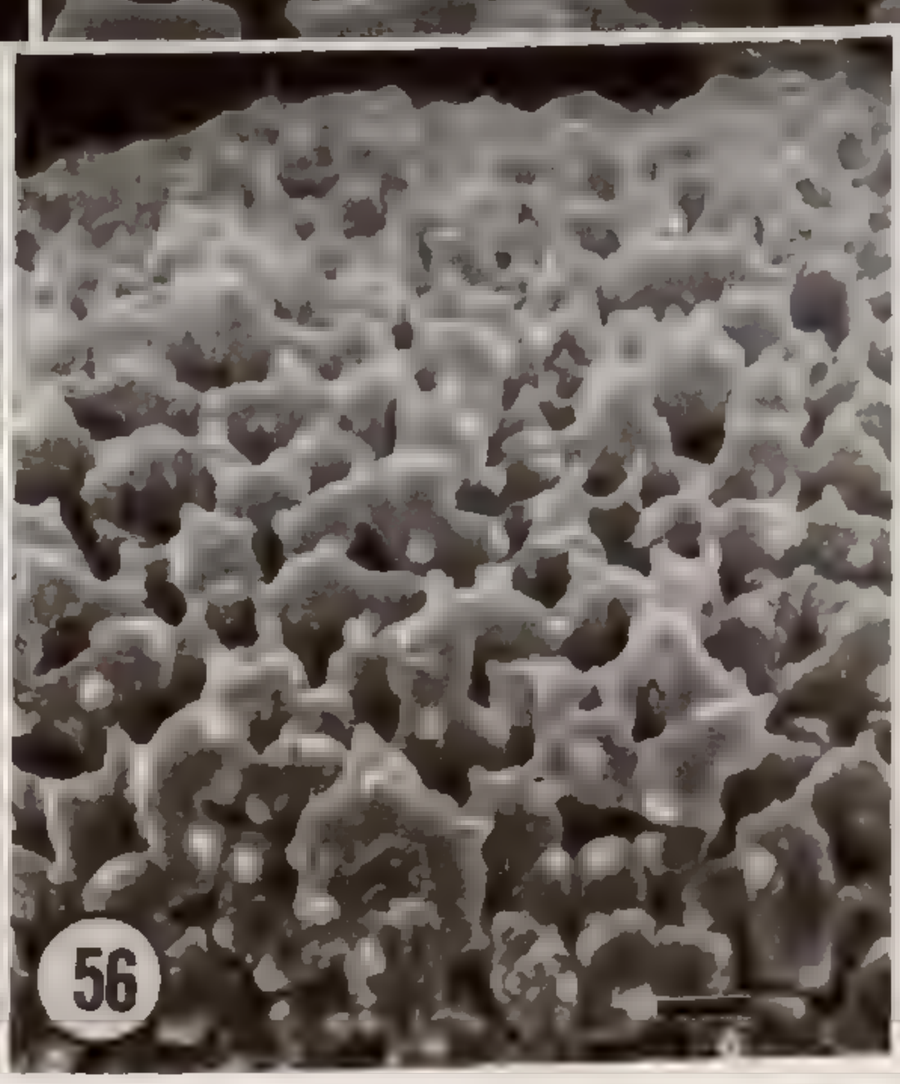




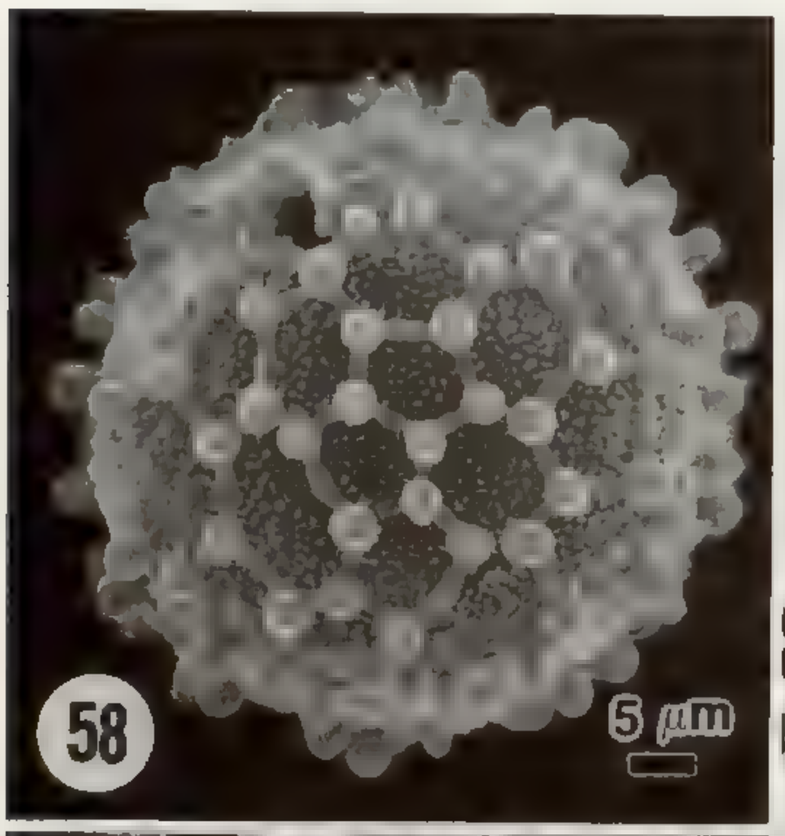


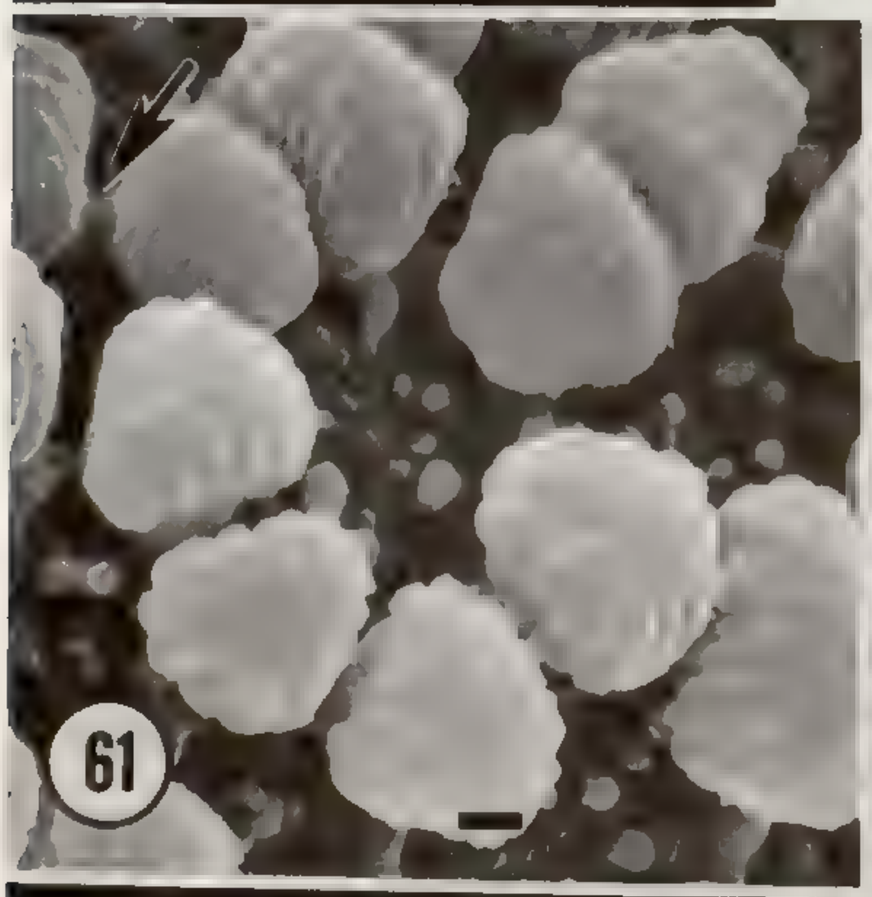


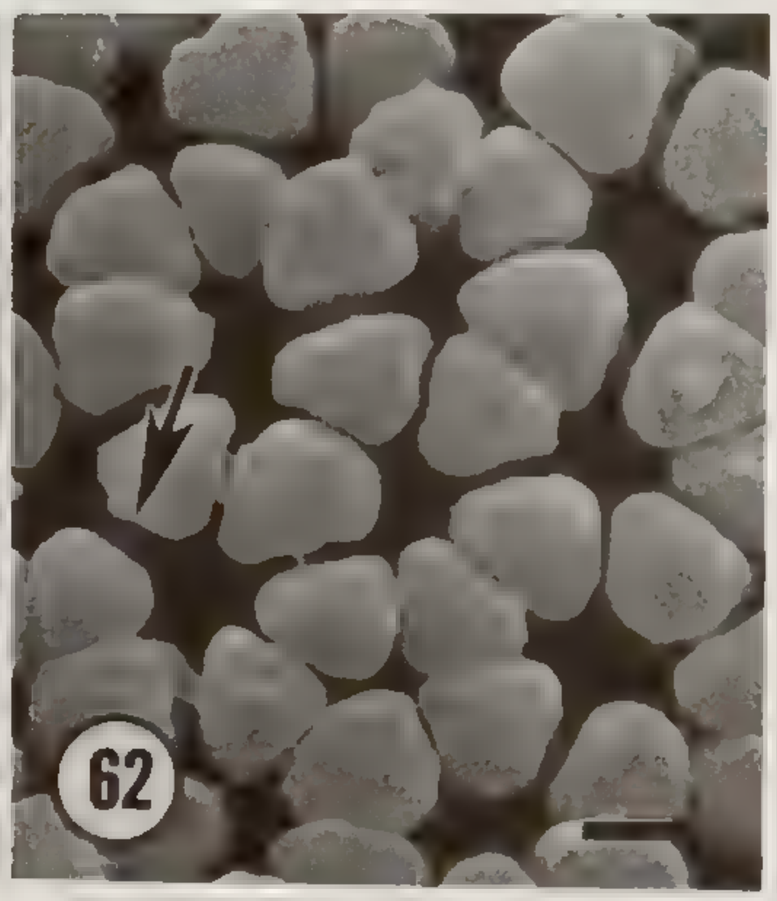


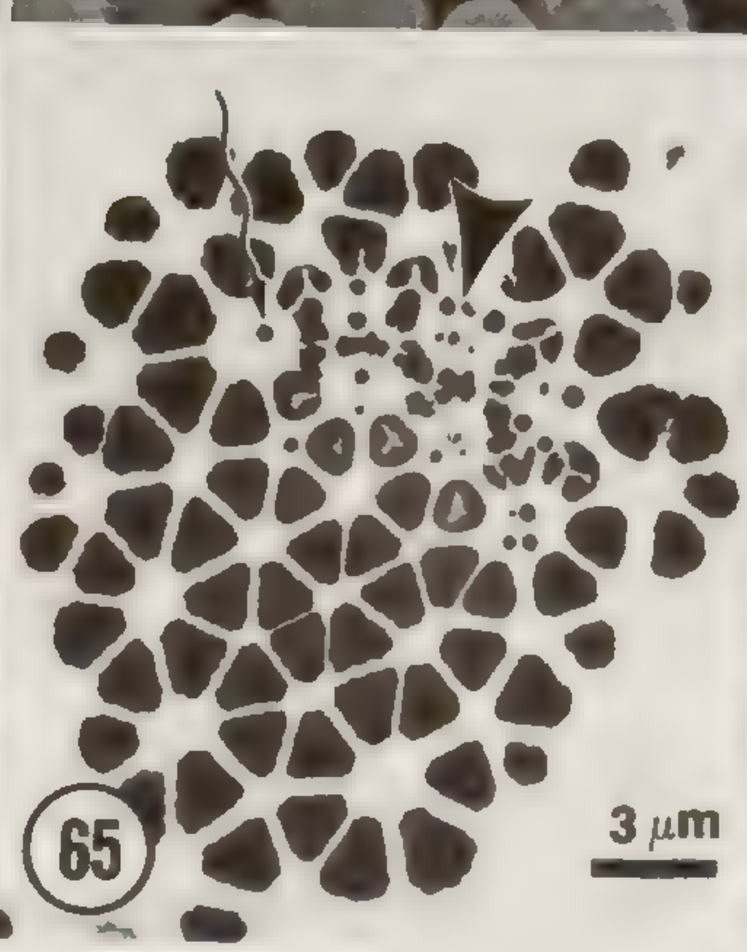


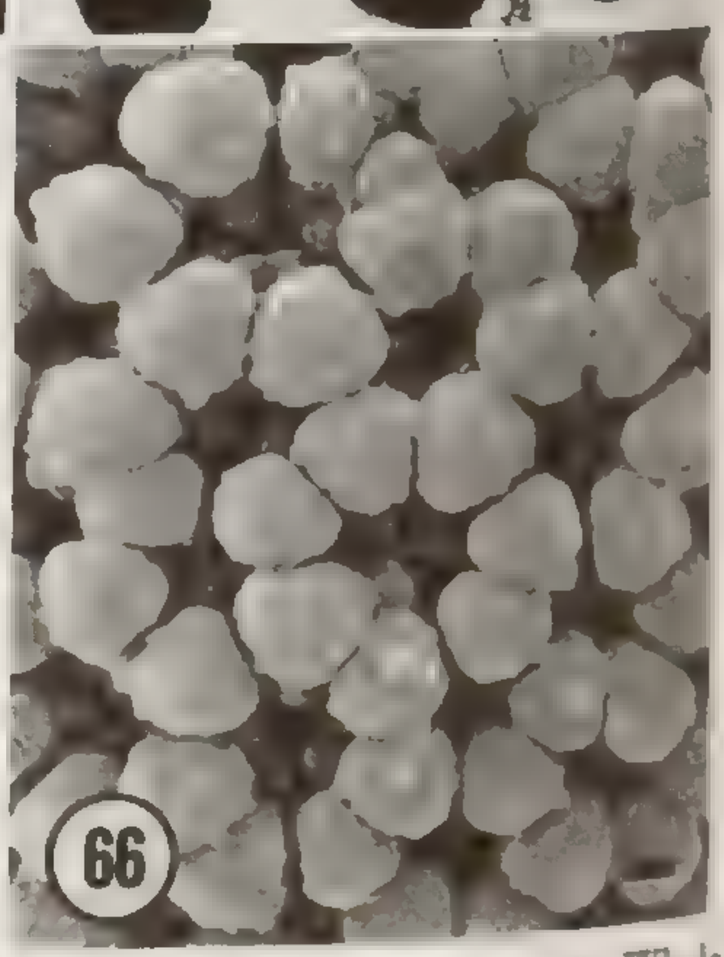
FIGURES 49–57. SEM and TEM of pollen in tribe Ricinocarpeae.—49. *Alphandia furfuracea*.—50. *Ricinocarpos glaucus*. Whole grain, partially collapsed.—51. *R. bowmannii*. Tectum. This species and *Croton matourensis* (Figs. 58, 59) have the most open tectal configuration of all Crotonoideae examined here. 52–54. *Beyeria leschenaultii*.—52. Whole grain.—53. Tectum. See discussion of Figure 54.—54. Radial section. Although subunits appear to rest on a trace of footlayer and thin lamellate endexine, no subunit examined in TEM is hollow; thus only the solid upper portion is the subunit. If the gaps (small arrowheads) were closed up, the muri would be recognizable.—55. *Ricinocarpos stylosus*. This species has a typical tectum. 56, 57. *Bertya gummifera*.—56. Tectum. This grain shows one of the more modified Croton structures—many subunits have fused together (another collection of this species is similar to the common structure).—57. Radial section. Note: paired columellae that support muri; granular footlayer; and thin, but well-delimited endexine.



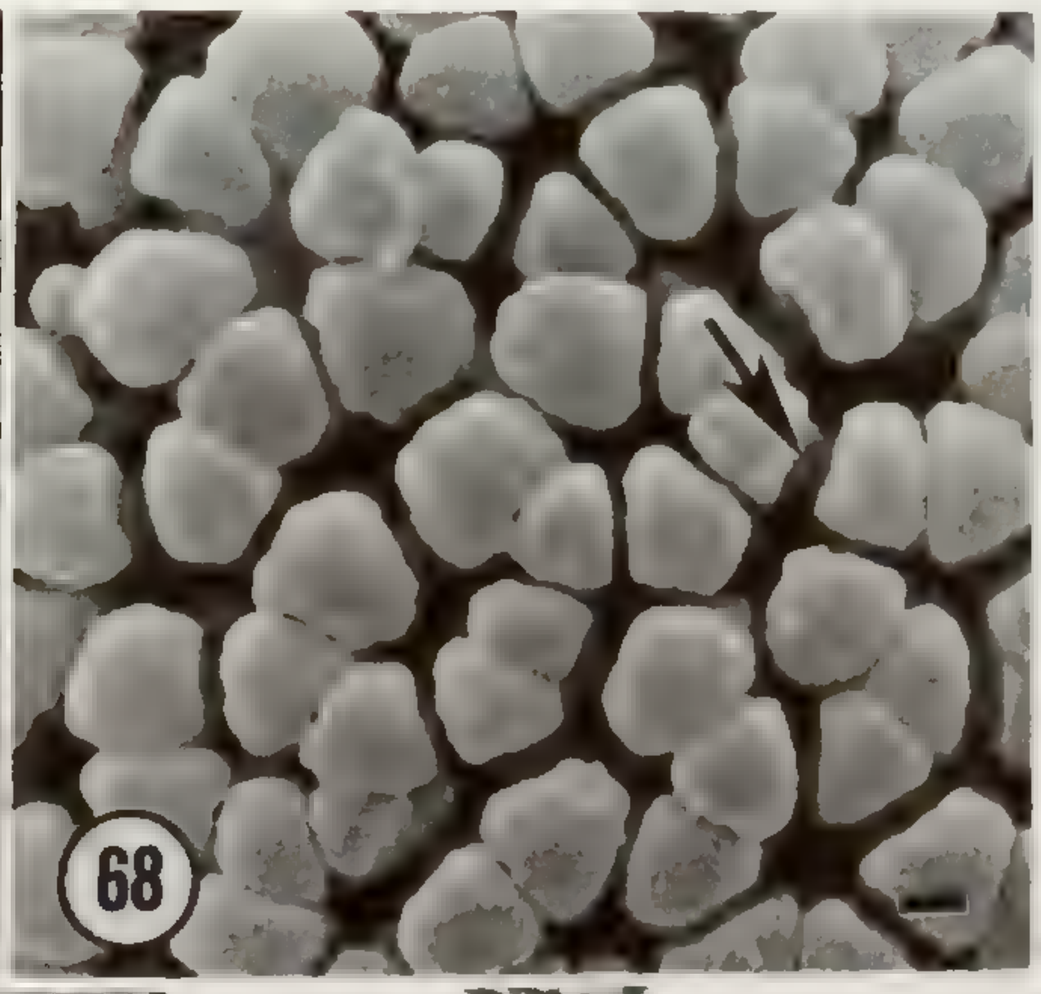


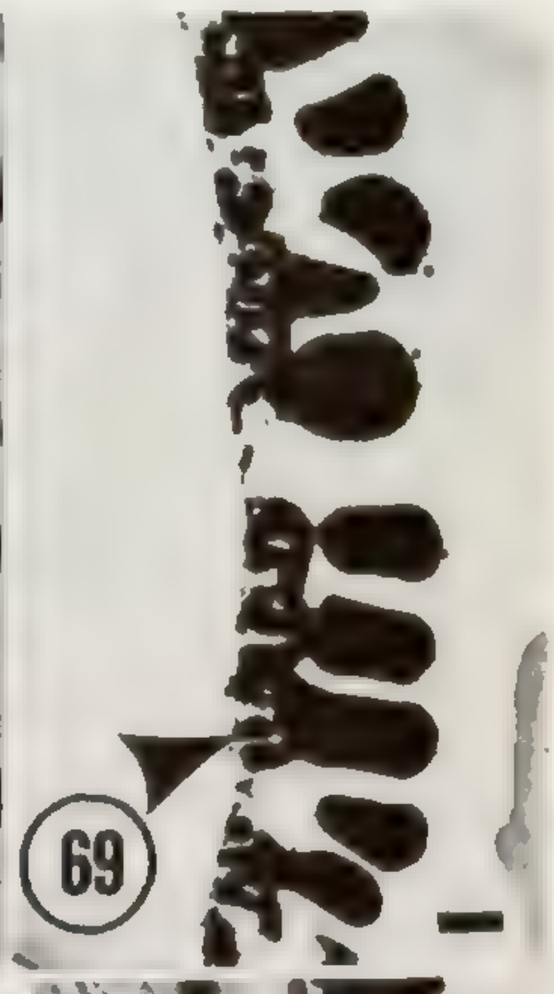


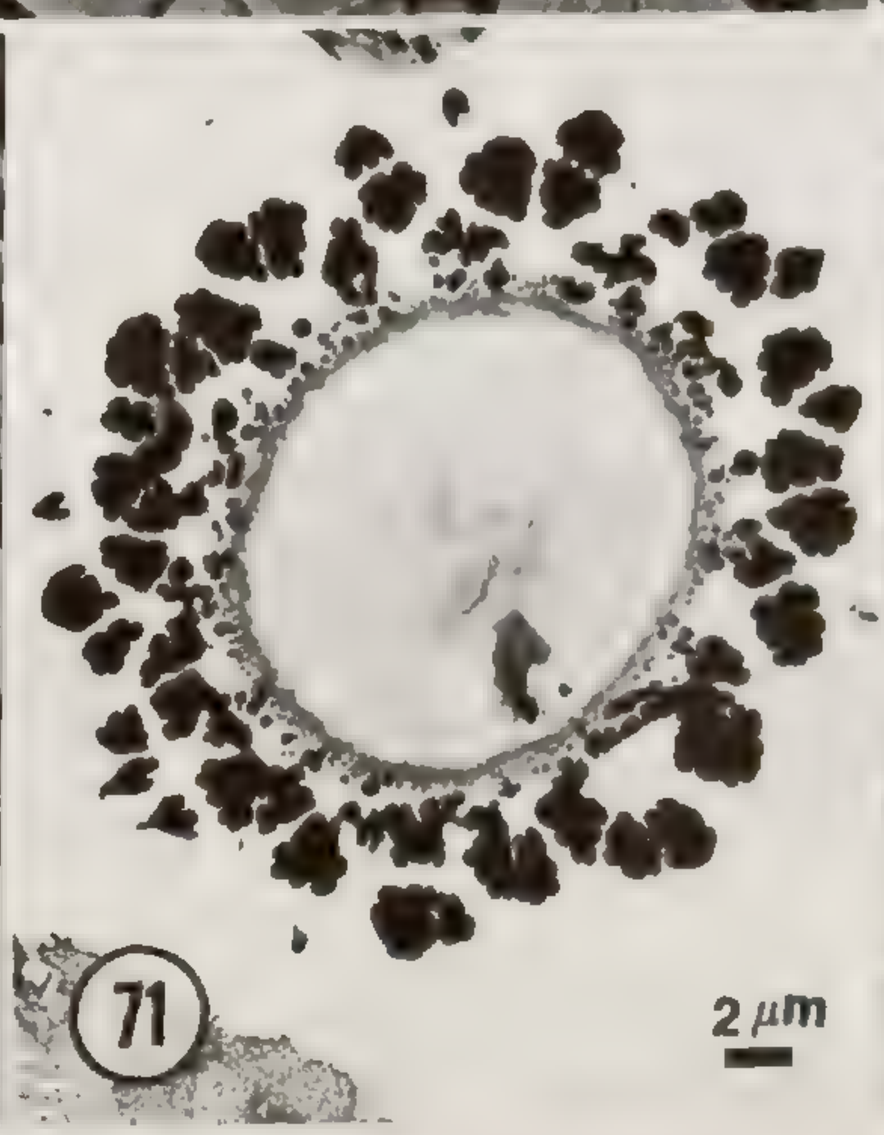


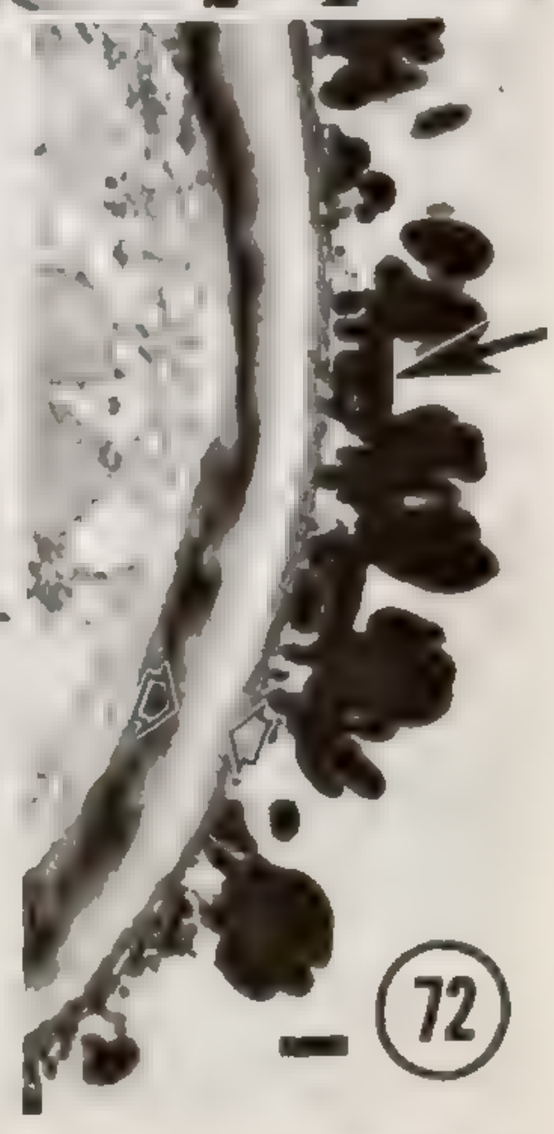


FIGURES 58–66. SEM and TEM of pollen in tribe Crotoneae, *Croton*. 58, 59. *C. matourensis*. —58. Whole grain. One of the most distinctive pollen morphologies in Crotonoideae, but a similar one occurs in *Ricinocarpos bowmannii* (Fig. 51). —59. Radial section. The vast majority of the surface area consists of lumina that have numerous fine granules above and below a very thin, irregular footlayer/endexine; two solid components at middle and left are muri cut at right angles to their long axes; at right is a large subunit cut in longitudinal section; although not readily apparent at this magnification, the thick muri rest on granules or granular columellae. —60. *C. balsamifer*. —61. *C. floribundus*. The lumina have scattered free columellae. 62, 63. *C. draco*. —62. Tectum. —63. Radial sections of two grains. Both have an irregular footlayer/endexine. —64. *C. pyramidalis*. The rounded apices and striate surface of the subunits are similar to Figure 61. 65, 66. *C. texensis*. —65. Tangential section. The thin muri show some evidence of paired columellae. —66. Tectum.

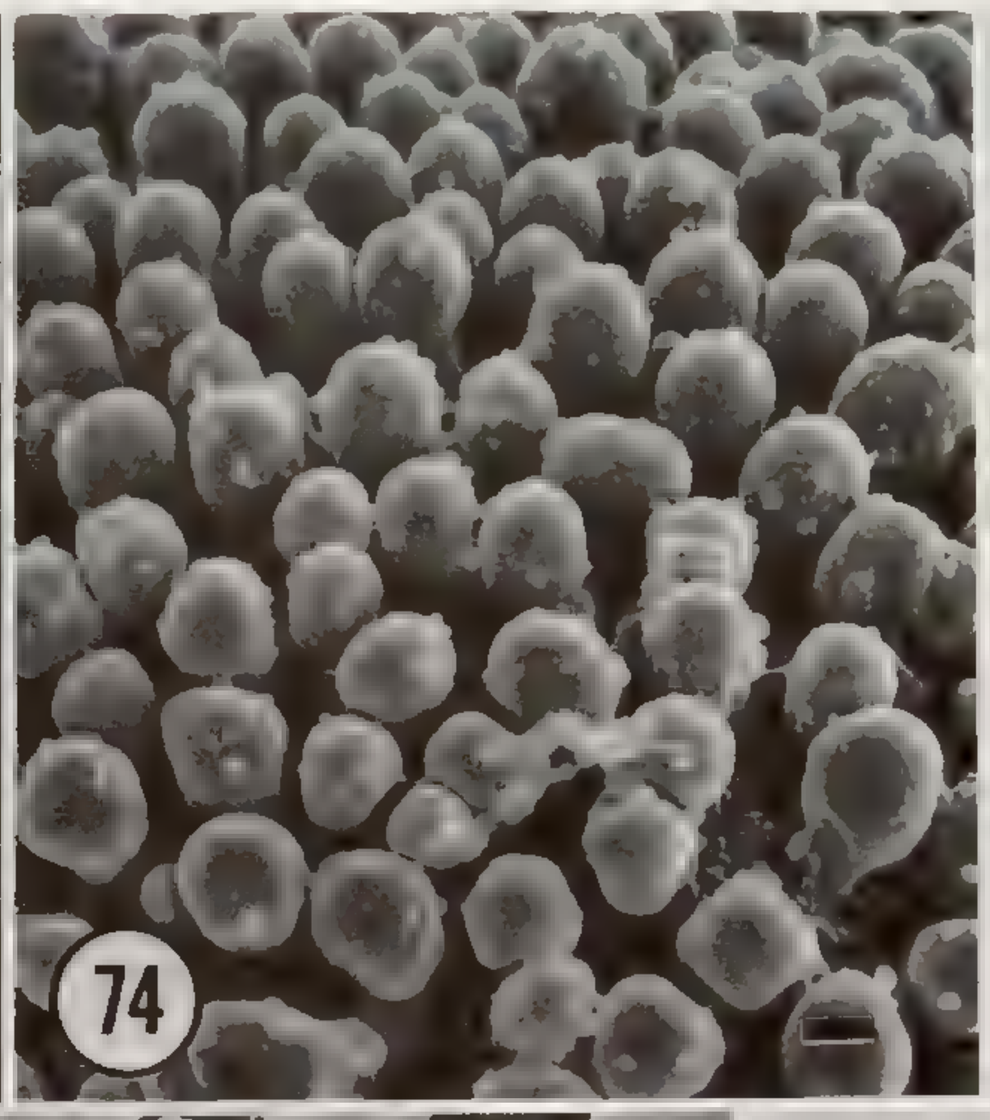


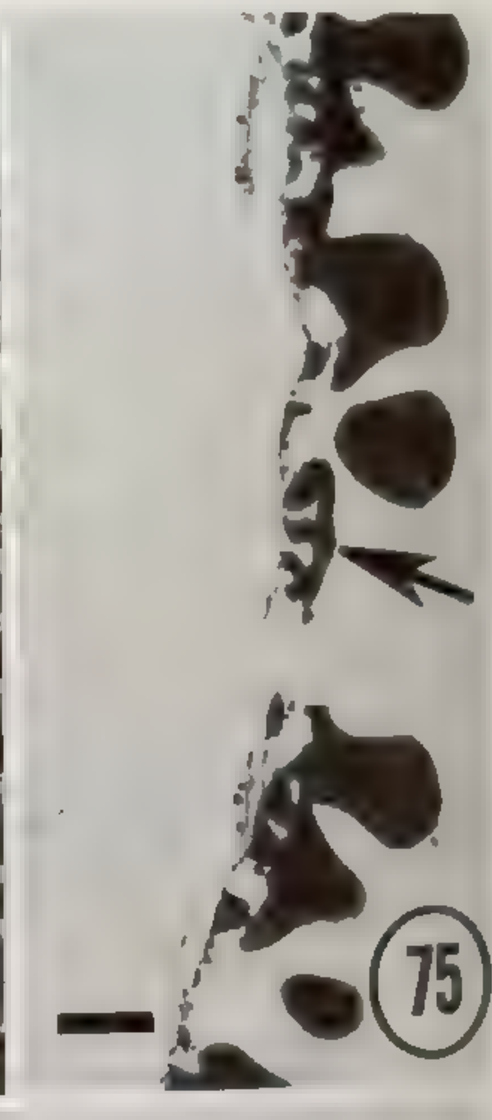


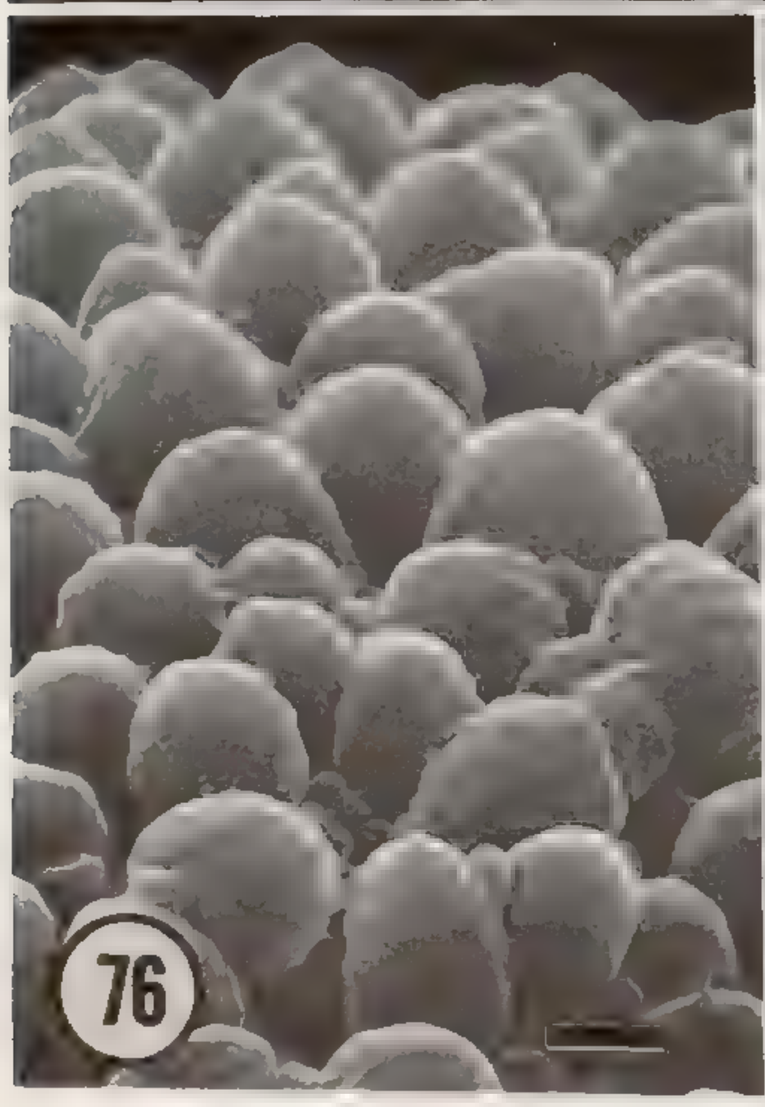


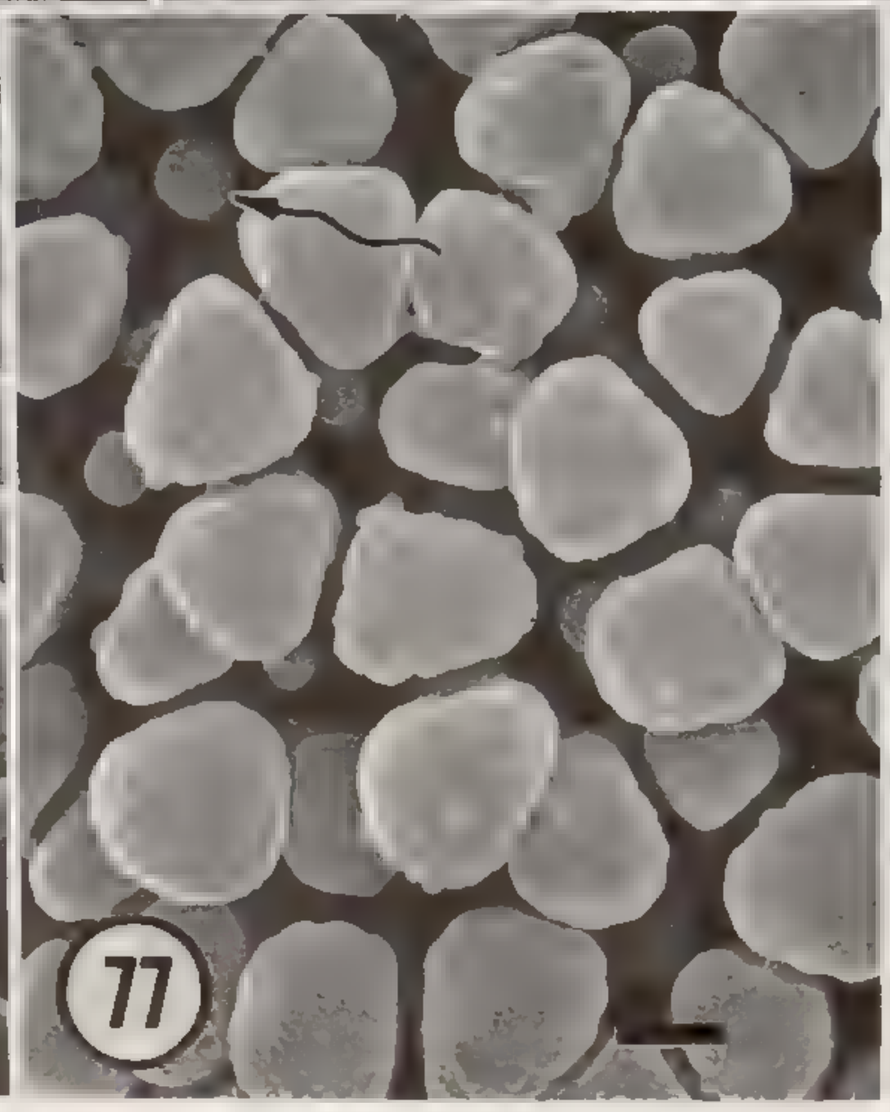


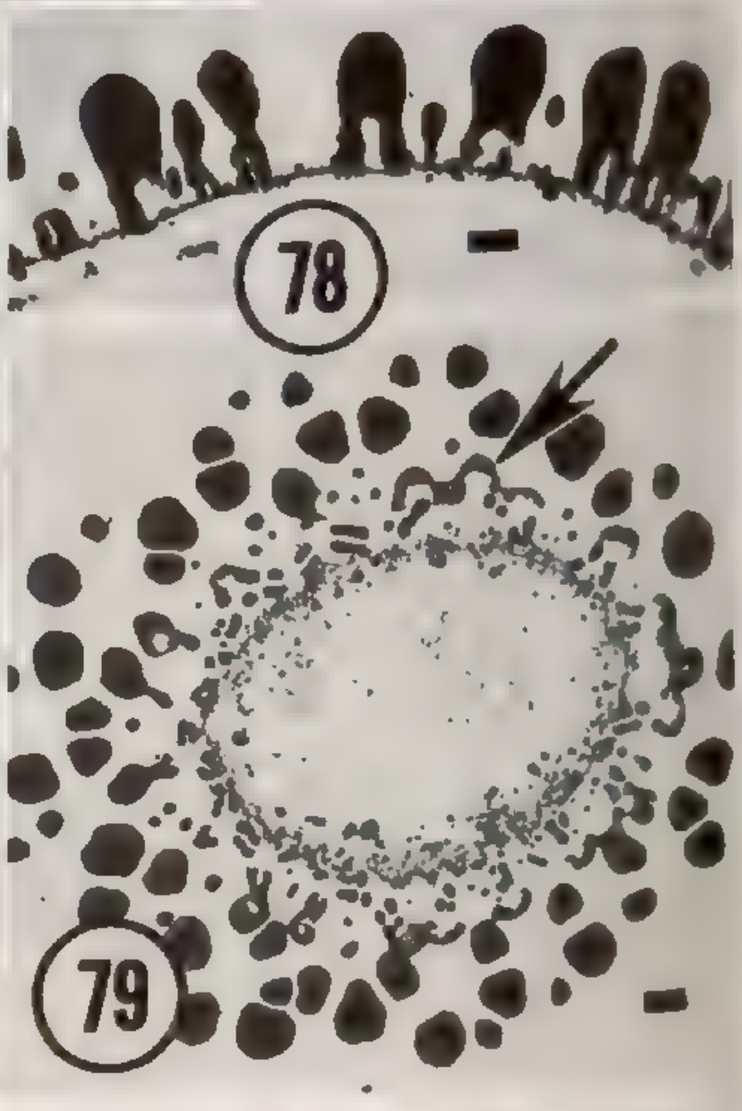
FIGURES 67–72. SEM and TEM of pollen in tribe Joannesieae. 67–69. *Joannesia princeps*.—67. Whole grain.—68. Tectum.—69. Radial section. Columellae here are well delimited; other sections show numerous granules above and below a trace of footlayer. 70–72. *Annesijoa novoguineensis*.—70. Tectum. Even though obscured by the deeply striate surface and elongate apices, at least some subunits (those in frontal view) show the basic triangular shape.—71. Tangential section. Even in tangential section, which enhances the thickness of layers, the footlayer is almost nonexistent, but the endexine is identifiable as the thin, innermost, less electron-dense layer.—72. Radial section of portion of incompletely acetolyzed grain; area between open arrowheads is assumed to be intine; note thin, but consistent, lamellate endexine; muri are much better demonstrated here than in Figure 71.



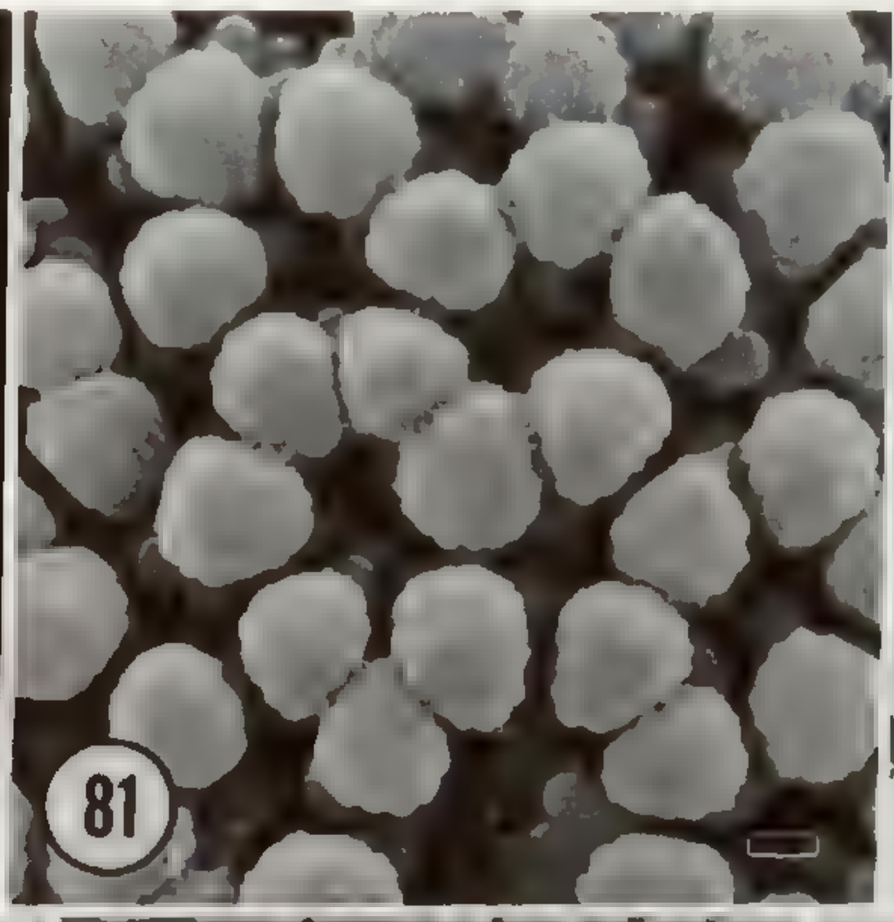


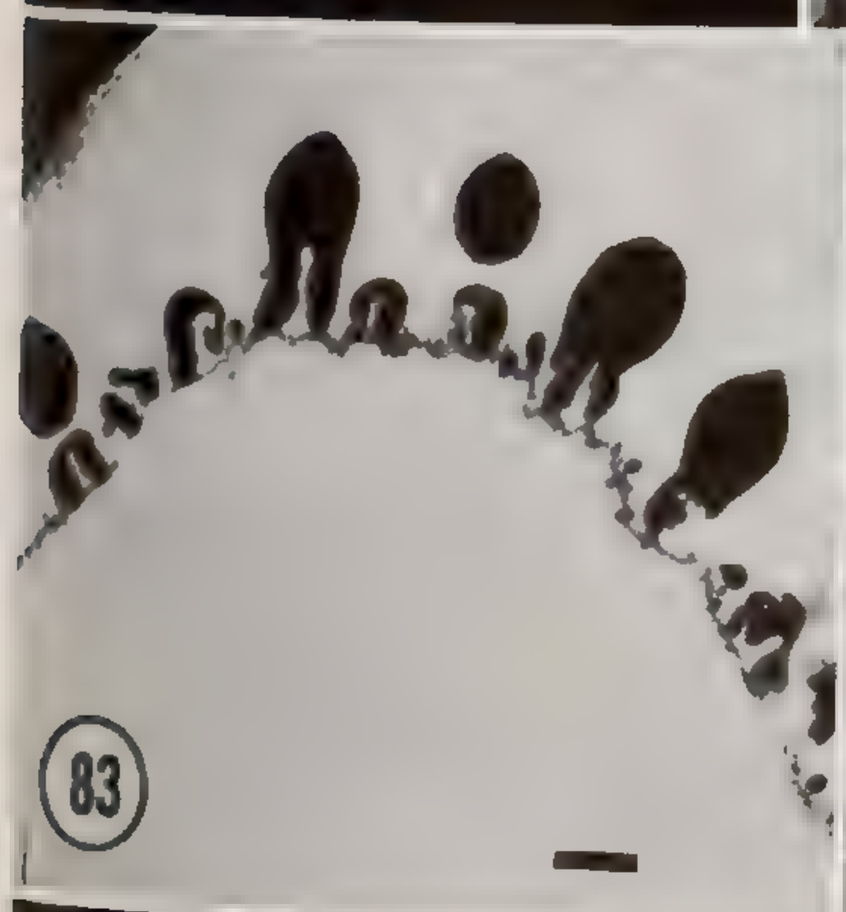


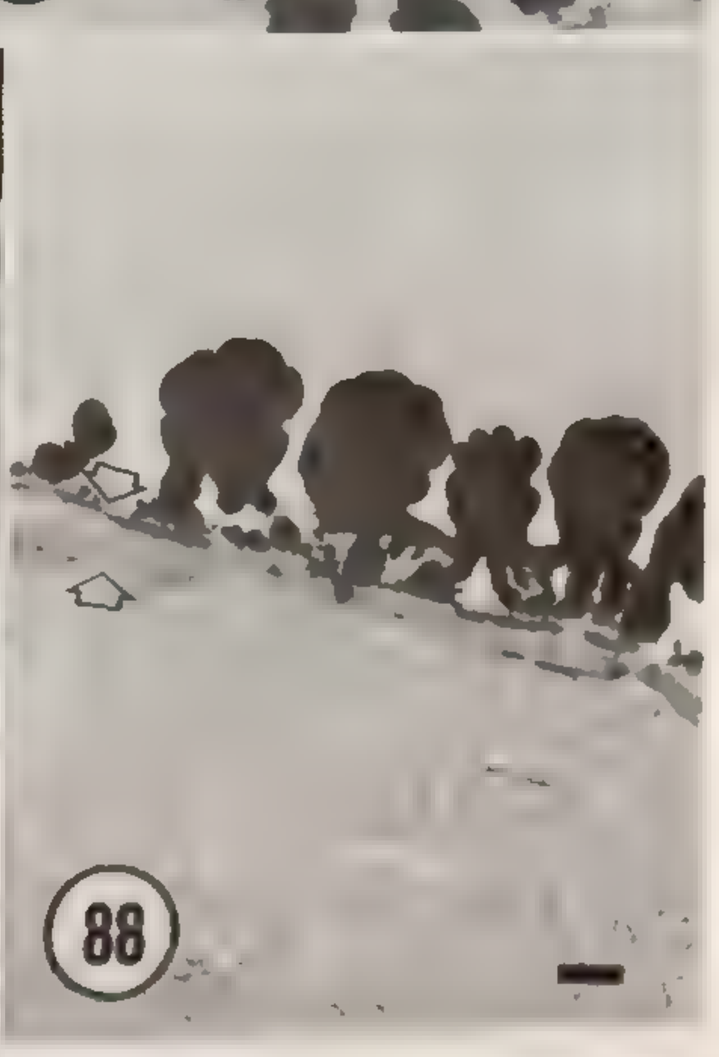




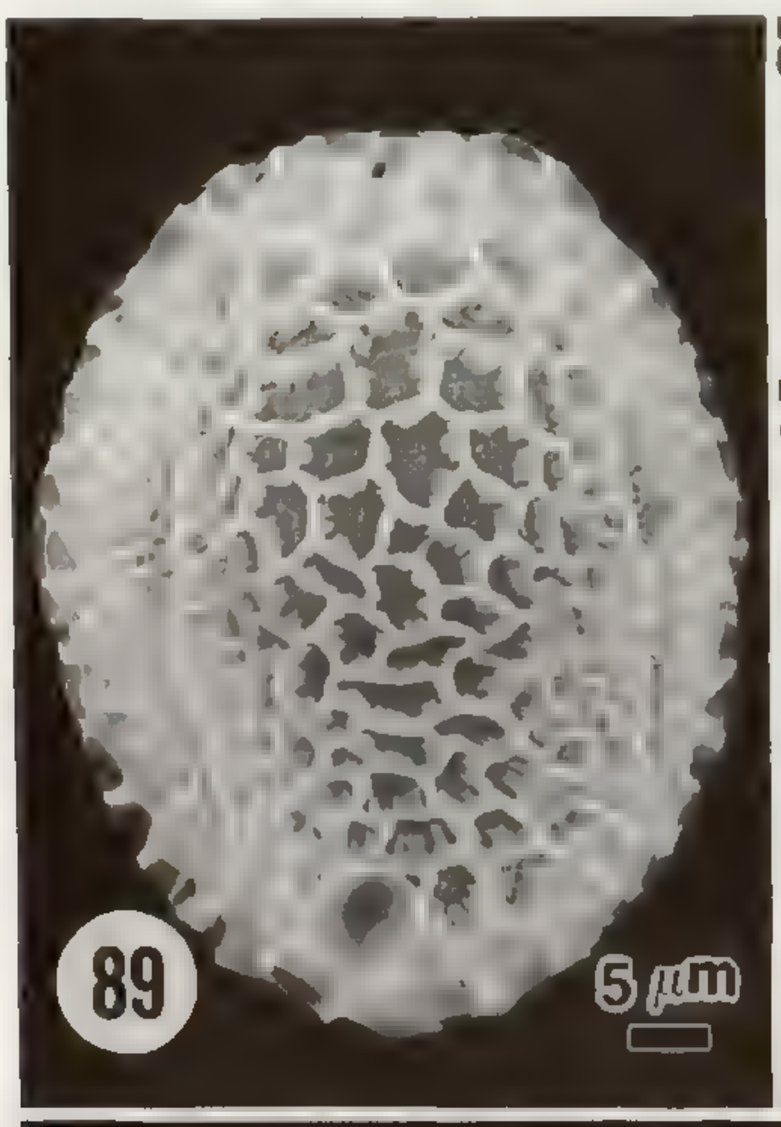
FIGURES 73–79. SEM and TEM of pollen in tribe Aleuritideae. 73–75. *Aleurites fordii*.—73. Whole grain.—74. Tectum.—75. Radial section. The footlayer/endexine are unusually thin, but other sections show numerous granules and a trace of footlayer. 76–79. *Ricinodendron rautanenii*.—76, 77. Tectal variation within pollen sample.—78. Radial section. The spacing of the subunits suggests that this grain is more like Figure 77 than Figure 76; note paired supporting columellae under center muri cut at a right angle to its long axis.—79. Tangential section. Muri are very thin; footlayer/endexine are highly irregular.

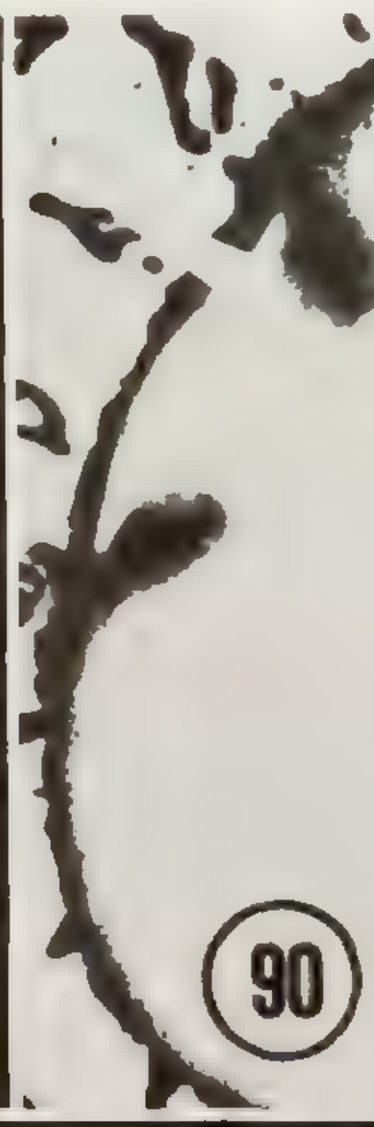


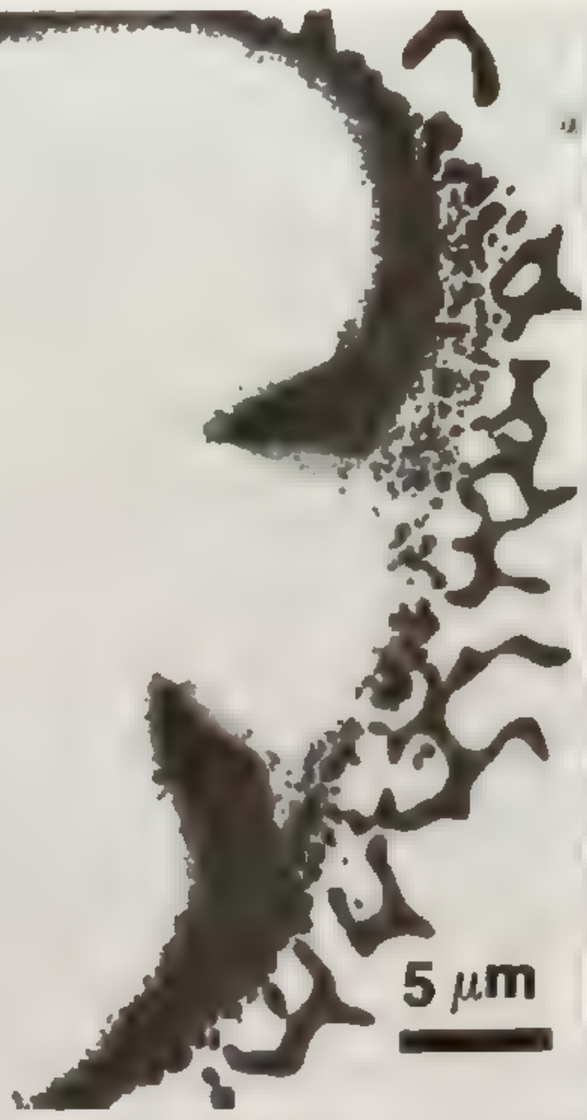


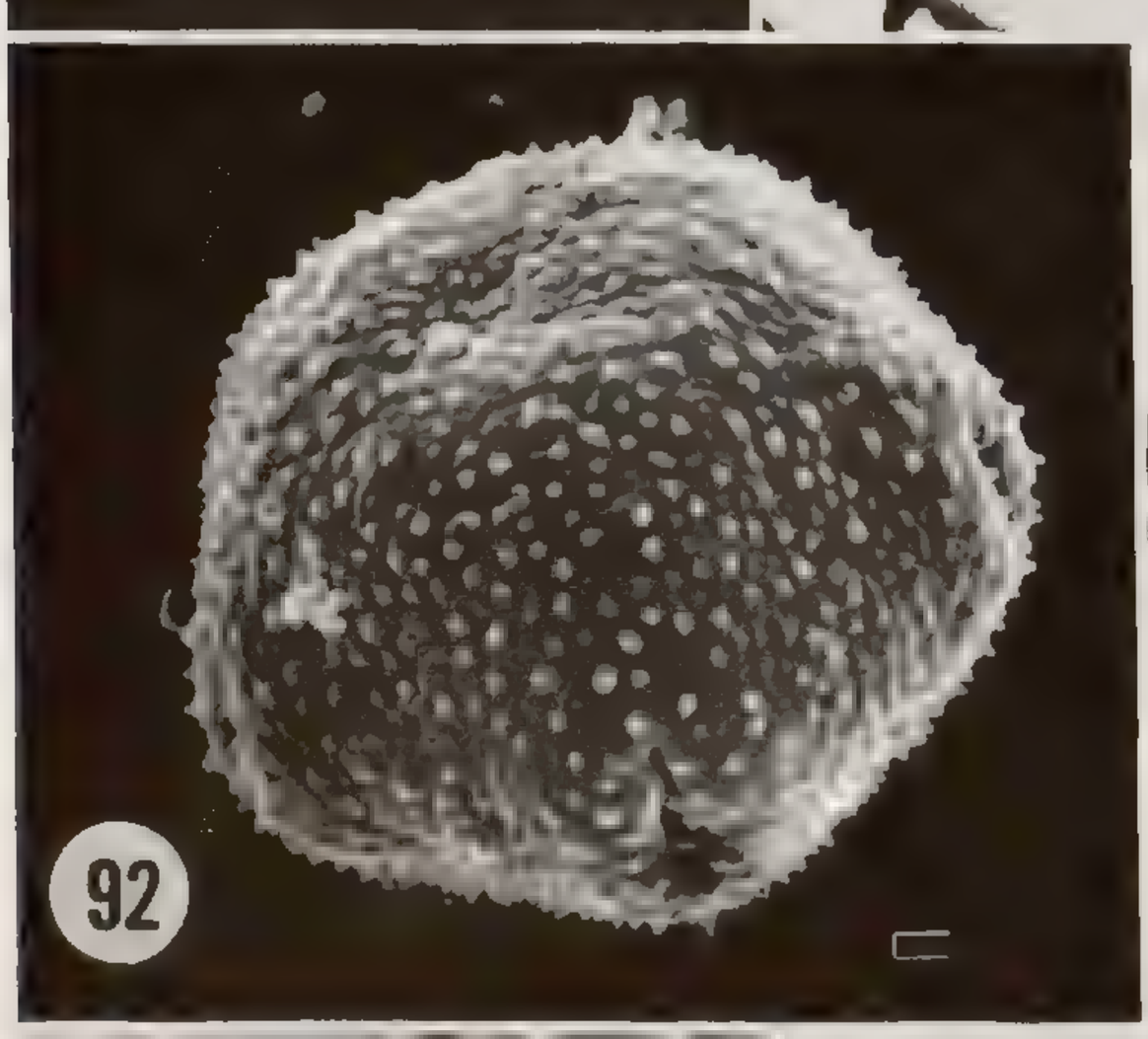


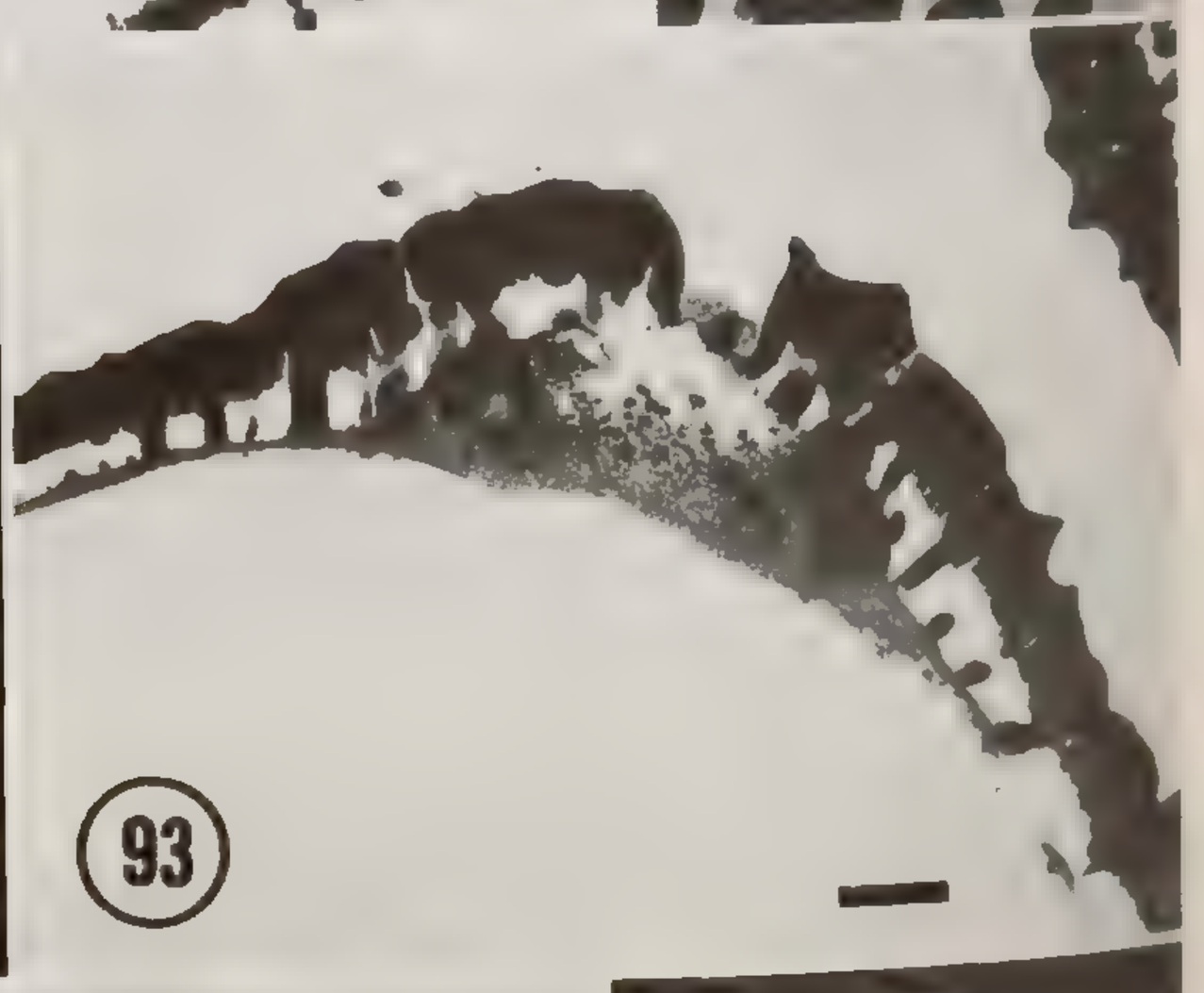
FIGURES 80–88. SEM and TEM of pollen in tribe Neoboutonieae. 80–82. *Anomalocalyx uleanus*. —80. Whole grain. —81. Tectum. —82. Radial section. Note thin muri and short columellae. 83, 84. *Grossera major*. —83. Radial section. The spacing of the subunits reflects the pattern in Figure 84; the muri have paired supporting columellae, the lumina have much smaller globules of ektexine. 85–88. *Crotonogyne argentea*. —85. Tangential section. Subunits reflect the deep striae illustrated in Figure 87. Small circles near center are free columellae cut in cross section; the section is not deep enough to include supporting columellae. —86. Whole grain. —87. Tectum. —88. Radial section. Like Figures 47 and 72, this grain is only partially acetolyzed, and the layer between the open arrowheads includes both endexine and intine.

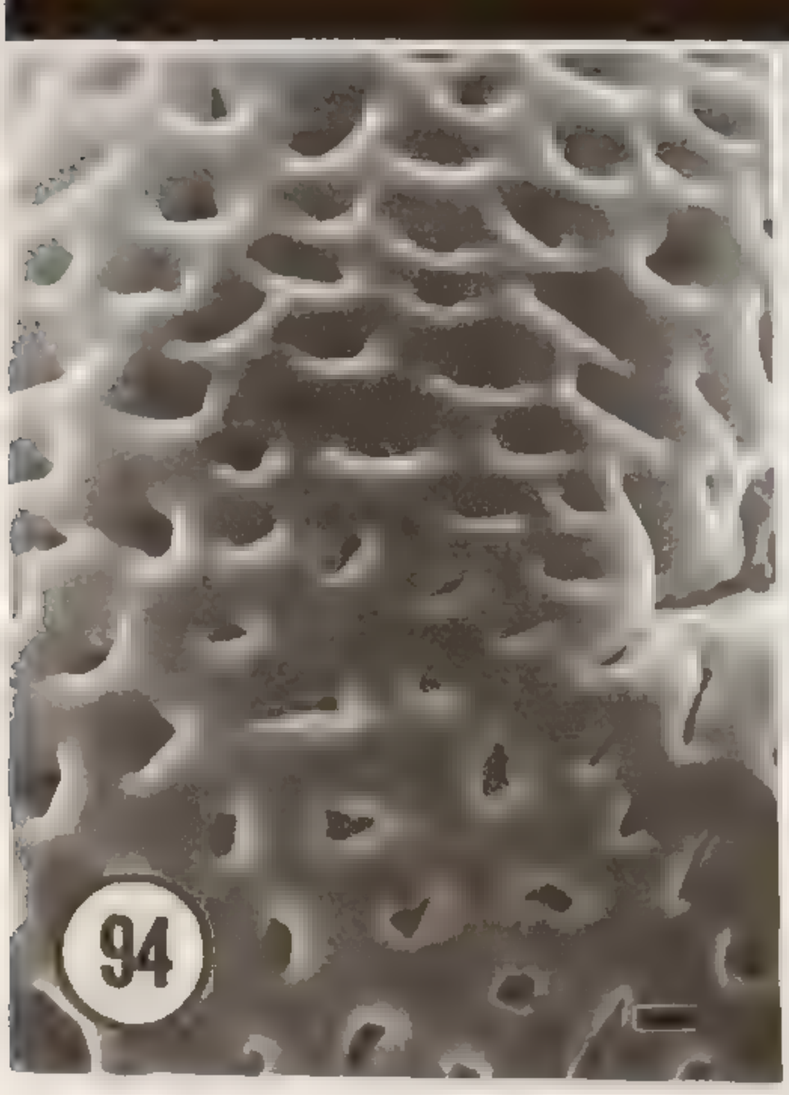


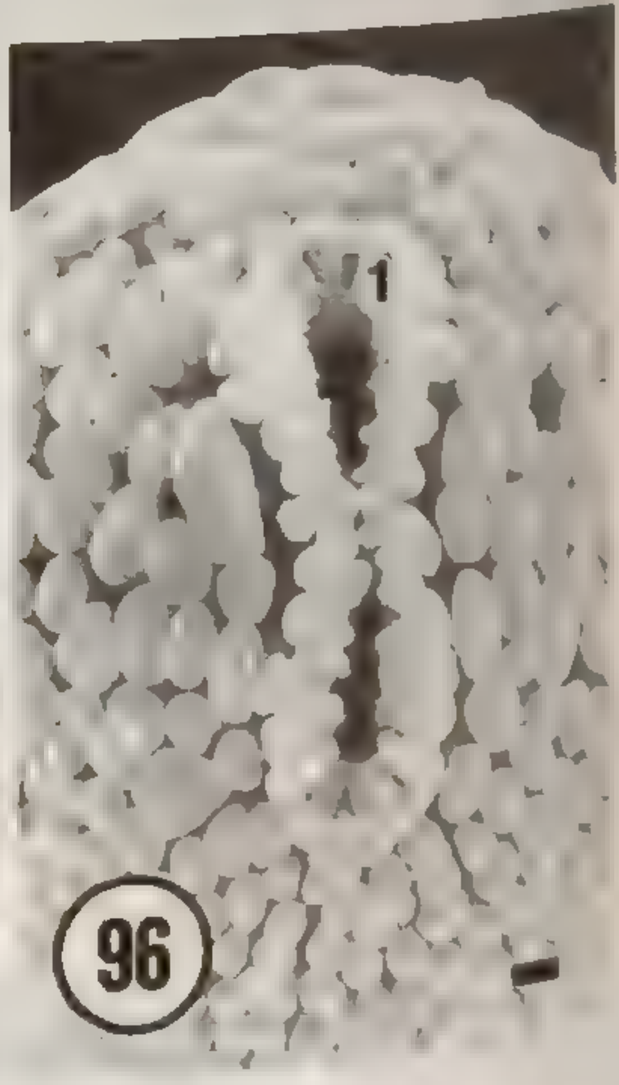




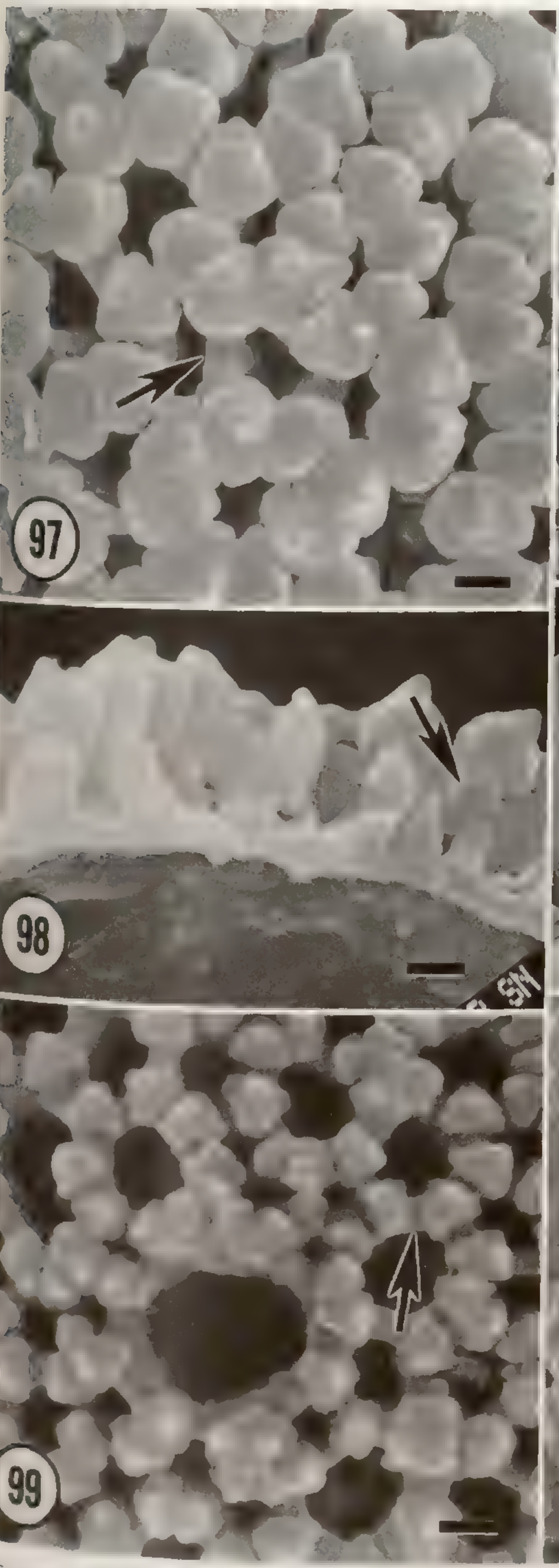


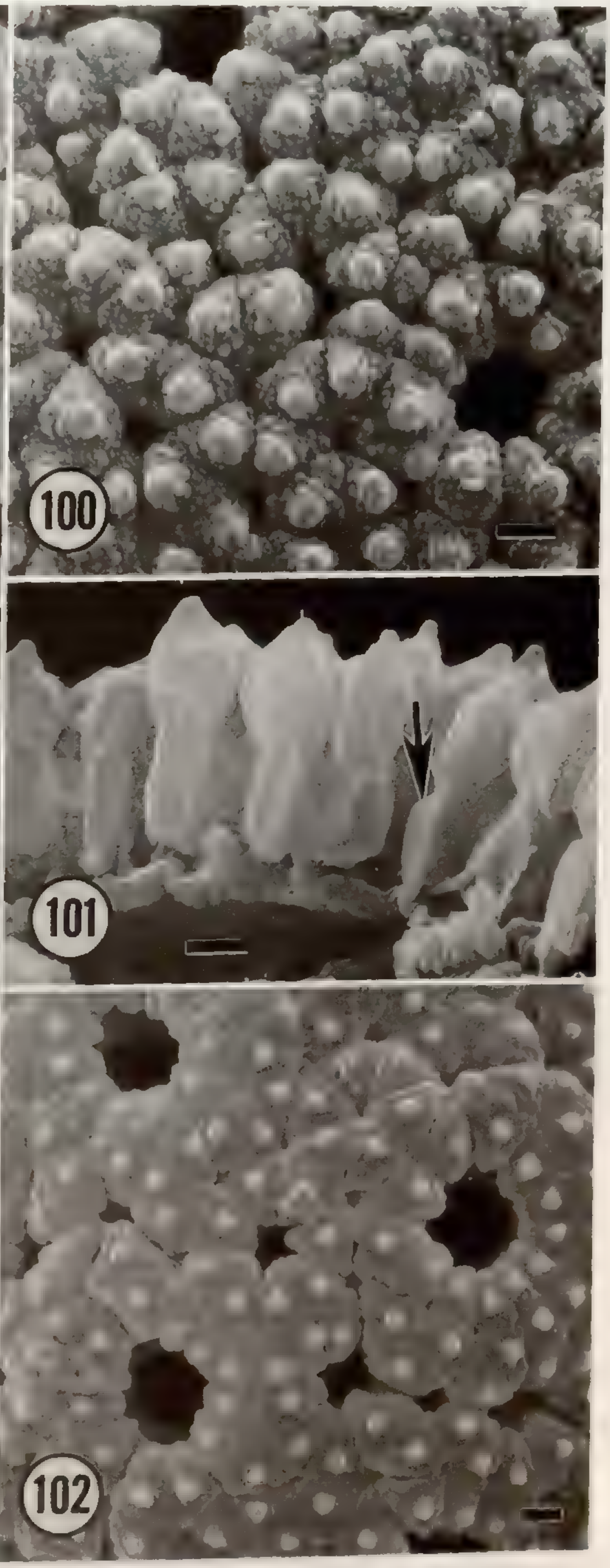






FIGURES 89–96. SEM and TEM of pollen of Euphorbiaceae. 89–91. Acalyphoideae. *Dalechampia humilis*. 89. Equatorial view. —90. Slightly oblique longitudinal section. Grain is 3-colporate and the zonorate endoaperture is delimited by very prominent costae. At right, section has passed along center of colpus and endoaperture; note prominent costae of equatorial band. —91. Tectum along colpus. 92, 93. Oldfieldioideae. *Longetia buxoides*. —92. Oblique view of an oblate, 5-brevicolporate grain. —93. Radial section through aperture. Note thick tectum, slender columellae, and at left and right, the thin footlayer/endexine; apertural thickening is partially footlayer (same electron density as the columellae and tectum) and partially endexine. 94, 95. Euphorbioideae. *Euphorbia pulcherrima*. 94. Tectum near pole. —95. Radial section of whole grain. Note elongate columellae, thin but consistent footlayer in mesocolpus, endexine accumulation under apertures, and perforate tectum. —96. Phyllanthoideae. *Phyllanthus acuminatus*. This unusual grain has three of these bordered "colpi" that are united midlength and a pilate tectum in which the pila at one pole are noticeably larger than at the other.





FIGURES 97–102.[3] SEM of pollen of Thymelaeaceae. 97, 98. *Gyrinopsis cumingiana*.—97. Tectum. Arrow marks muri.—98. Fracture. Arrow marks broken muri.—99. *Schoenobiblus grandifolia*. Tectum including pore.—100. *Pimelea prostrata*. The close spacing of subunits obscures muri.—101. *Gnidia glauca*. Fracture illustrating broken edges (arrow) of vertically elongated muri.—102. *Pimelea ligustrina*. Tectum.

LATICIFERS IN CROTONOIDEAE (EUPHORBIACEAE): HOMOLOGY AND EVOLUTION[1]

Paula Rudall[2]

Abstract

Laticifer distribution is described in several genera of Euphorbiaceae, particularly in subfamily Crotonoideae, previously neglected in this respect. Branched, nonarticulated laticifers are common in both Crotonoideae and Euphorbioideae, sparse in Acalyphoideae (occurring in, e.g., *Omphalea*), and absent in the other two subfamilies. However, many genera without latex have elongated, highly branched sclereids in the mesophyll, which may in some instances be homologous with laticifers. Typical articulated laticifers (consisting of numerous fused cells) are currently known in only three genera of Crotonoideae, although several anomalous and transitional forms are reported. Crotonoideae differs from Euphorbioideae in that nonarticulated laticifers originate in the protophloem, and are in general more abundant in the phloem, in common with articulated laticifers. Laticifer evolution is discussed in relation to the phylogeny of Euphorbiaceae.

The objectives of this investigation are to assess the phylogenetic significance of laticifers in Euphorbiaceae with particular reference to the subfamily Crotonoideae and to a lesser extent Acalyphoideae, both less well known than Euphorbioideae in this respect (Rudall, 1987). Ontogenetic data are important in this type of investigation, but are limited by the availability of sufficient material. The role of ontogenetic data in systematics has seen a recent resurgence of interest, especially with respect to the establishment of homologies of features present at maturity. This aspect has particular relevance to a study of laticifers, where development is important in the classification of the different types. Most recent investigations of laticifer development in Euphorbiaceae have concentrated on *Euphorbia* and closely related genera in Euphorbioideae (e.g., Mahlberg & Sabharwal, 1968). Developmental studies on other genera are scanty, largely owing to the difficulty of obtaining suitable material. Those that do exist (e.g., Chauveaud, 1891; Gaucher, 1902) need updating in the light of modern methods and taxonomic concepts. Chauveaud (1891) examined several genera of Euphorbioideae and three species of Crotonoideae, *Aleurites triloba*, *Croton pungens*, and *Jatropha curcas*, but without illustrations. Scott (1884a, b, 1886) examined articulated laticifers in embryos of *Manihot* and *Hevea*, both Crotonoideae.

Webster (1975) used latex production and presence or absence of laticifers as characters in his classification of Euphorbiaceae into five subfamilies; however, information on both is frequently lacking in the literature. Records of latex exudation indicate the presence of laticifers, but lack of such records may simply mean that the latex, if present, is not conspicuous. Latex is of very widespread occurrence among Crotonoideae and Euphorbioideae, but varies in color and abundance. Milky, whitish sap is particularly characteristic of Euphorbioideae; in *Euphorbia phosphorea* this even becomes phosphorescent on exposure (Spix & Martius, 1828). Among Crotonoideae, although some genera have white latex (such as *Manihot* and *Hevea*, genera with articulated laticifers), many others, such as *Aleurites*, *Codiaeum*, and *Neoboutonia*, have a clear, often viscous, latex. Red latex occurs in occasional species of several genera, such as *Alphandia*, *Baloghia*, *Cocconerion*, *Croton*, *Endospermum*, and *Pausandra* (McPherson & Tirel, 1987; Roosmalen, 1985; Schaeffer, 1971).

[1] I thank the following for supplying fresh material: Director, Adelaide Botanic Garden, Australia; Director, National Botanic Gardens, Zimbabwe; Curator, Mount Coot-tha Botanic Gardens, Queensland, Australia; Director, Jardín Botánico National, La Habana, Cuba; K. Alvin, Imperial College, London (material of *Androstachys johnsonii*); D. C. Lees (material from Panama and Cameroon). I am also very grateful to T. Lawrence (Jodrell Laboratory), P. Burns (Thames Polytechnic), and S. Hewis (Hatfield Polytechnic) for technical assistance and discussion, C. J. Humphries (British Museum, Natural History) for comments on the manuscript, and R. M. Harley (Royal Botanic Gardens, Kew) and A. M. Giulietti (University of São Paulo) for help in the field.

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There are also records of latex in Acalyphoideae: species of *Omphalea* exude a clear or slightly milky latex, which oxidizes to red; *Macaranga* has latex ranging from clear to yellow, orange, or red (McPherson & Tirel, 1987).

Apart from a few scanty records in Acalyphoideae, laticifers are documented only in subfamilies Euphorbioideae and Crotonoideae (Rudall, 1987). Two laticifer types occur in Euphorbiaceae—articulated (chains of fused cells; recorded in a few genera of Crotonoideae only, e.g., *Hevea*) and nonarticulated (individual cells with intrusive growth, e.g., in *Euphorbia*, and many other genera). Some authors (e.g., Metcalfe, 1967) have regarded this as evidence of polyphyly. Indeed, Mahlberg et al. (1987) proposed that Euphorbiaceae should be regarded as three distinct families, one lacking laticifers, one with articulated laticifers, and one with nonarticulated laticifers, although most recent classifications (e.g., Webster, 1975) would reject this on the basis of other characters.

Materials and Methods

Material was obtained from various sources (Table 1). Herbarium material (dried leaves) was from the herbarium of the Royal Botanic Gardens, Kew (K). Leaves (L), stems (S), and in some cases, apices, fixed in formalin acetic alcohol (FAA), were acquired from the author's own collections in Brazil, living collections at Kew (HK), Limbe Botanic Garden, Cameroon, and the Smithsonian Tropical Research Institute (STRI), Panama. Seeds for embryo examination (E) were obtained from the Kew spirit collection (SC), Kew living collections (HK), other botanic gardens, and the author's own collections in Brazil. In many instances apparently sound seeds were found to lack embryos, or the embryos were not sufficiently well preserved for inclusion in this survey.

Fresh material was fixed in FAA for at least 48 hours, then stored in 70% alcohol. Herbarium material was revived by boiling in water. Leaves and stems were sectioned using a Reichert sliding microtome. Embryos and apices were embedded in Paraplast using standard methods of wax embedding, and sectioned using a Reichert rotary microtome. Sections were stained in safranin and Alcian blue, dehydrated through an alcohol series, and mounted in Euparal. Leaf fragments of *Codiaeum variegatum* were macerated by transferring them to a flask containing a mixture of equal parts of glacial acetic acid and 20-volume hydrogen peroxide, heating the mixture on a water bath for about 8 hours, then shaking it vigorously to achieve cell separation.

Observations

Embryos

The distribution of nonarticulated laticifer initials in the Crotonoideae embryos examined here (excluding *Hevea confusa*) corresponds to the classical concept of initiation of nonarticulated laticifers (Schmalhausen, 1877), and is broadly consistent with records of development in *Euphorbia* and other Euphorbioideae, and indeed for nonarticulated laticifers in other dicotyledon families. Nonarticulated laticifer initials are present in the pericyclic region of the embryonic cotyledonary node, at a variable number of points around the axis. They subsequently permeate throughout other tissues by rapid intrusive growth, as Mahlberg & Sabharwal (1968) demonstrated in *Euphorbia*. Among different species of *Euphorbia* the number of initials varies from 4 or 8 to 12 or more (Chauveaud, 1891), the variation probably relating to differences in embryo size and number of primary vascular bundles in the different species. In mature embryos observed here the pericyclic ring consists of only ca. 8 initials in *Synadenium grantii* (Euphorbioideae) (Figs. 5, 6), but generally more in Crotonoideae: e.g., ca. 24 initials in *Baloghia lucida* (Fig. 2), *Croton megalobotrys*, *C. sylvaticus*, and a much larger number in *Aleurites triloba* (Fig. 8), although these may have proliferated by this stage. Furthermore, in Crotonoideae the initials occur toward the outer edge of the procambial tissue (i.e., within the protophloem region), contrary to the situation in Euphorbioideae (e.g., *S. grantii*, Figs. 5, 6), where they originate on the outside edge of the provascular tissue, as Mahlberg & Sabharwal (1968) also noted in *Euphorbia*. Initials elongate and branch intrusively, forming a complex laticiferous network. In *Baloghia lucida* the initials are considerably larger than surrounding cells (Figs. 3, 4), indicating possible polyploidy, although there is no evidence for this. Branches of the initials extend to the subepidermal region of the embryonic axis and toward the radicle (Fig. 1), thus forming two separate laticiferous rings, as de Bary (1884) and Chauveaud (1891) also noted in *Euphorbia*. Two distinct concentric rings (Fig. 7) were seen here in the hypocotyls of species of both Euphorbioideae (*Euphorbia lathyris* and *Synadenium grantii*) and Crotonoideae (*Baloghia lucida*, *Croton* spp.). Further branches proliferate around the cotyledonary node, close to the apex, and extend upwards into the cotyledons.

Mature embryos of *Hevea confusa* have a very short hypocotyledonary stem and two large broad cotyledons (Fig. 9). Typical articulated laticifers

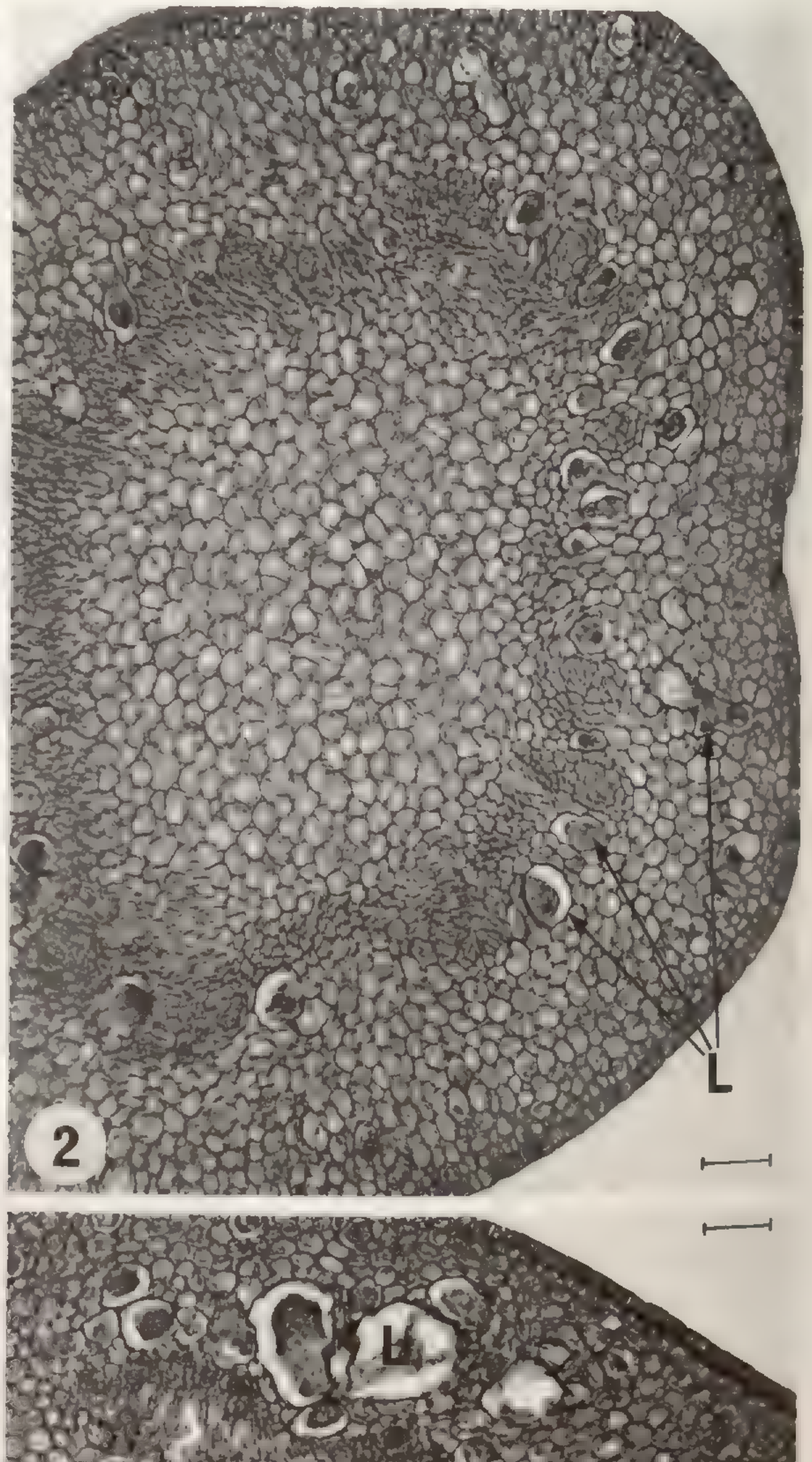
TABLE 1. Taxa and material examined, with observations on laticifers and sclereids.

Taxon	Source & data[a]	Plant part[b]	Laticifers[c]	Sclereids in leaves[c]
Acalyphoideae				
Omphalea diandra L.	cult. STRI, Panama	LS	+ nonarticulated	–
Omphalea triandra L.	cult. STRI, Panama	LS	+ nonarticulated	–
Omphalea oleifera Hemsl.	cult. STRI, Panama	LS	+ nonarticulated	–
Mallotus subulatus Muell. Arg.	Limbe B.G., Cameroon	L	–	+
Crotonoideae				
Adenocline acuta Baill.	K: Muller & Scheepers 47	L	+ nonarticulated	–
Aleurites triloba J. R. Forster & G. Forster	HK: Hyland 2696	LS, E	+ nonarticulated	–
Baloghia lucida Endl.	Adelaide B.G., Australia	LS, E	+ nonarticulated	–
Bertya mitchellii (Sond.) Muell. Arg.	K: Sharrad 779	L	+ nonarticulated	–
Beyeria leschenaultii (DC.) Baill.	K: Rohrlach 408	L	+ nonarticulated	–
Codiaeum variegatum (L.) A. Juss.	HK (no data)	LS	+ nonarticulated	+ (older leaves)
Croton antisyphiliticus Mart. ex Muell. Arg.	Brazil: Harley et al. 25010 (K)	LS	+ nonarticulated	–
Croton comosus Muell. Arg.	Brazil: Harley et al. 25109 (K)	LS	+ nonarticulated	–
Croton conduplicatus Kunth.	Brazil: Harley et al. 25156 (K)	LS	+ nonarticulated	–
Croton heteropleurus Urb.	cult. Cuba B.G.	LS	+ nonarticulated	–
Croton megalobotrys Muell. Arg.	Z: Muller 818	LS, E	+ nonarticulated	–
Croton occidentalis Muell. Arg.	Brazil: Harley et al. 24827 (K)	LS	+ nonarticulated	–
Croton sagreanus Muell. Arg.	cult. Cuba B.G.	LS	+ nonarticulated	–
Croton sylvaticus Hochst.	Z: Ritchken s.n.	LS, E	+ nonarticulated	–
Croton sp.	Brazil: Harley et al. 24832 (K)	LS	+ nonarticulated	–
Croton sp.	Brazil: Harley et al. 25091 (K)	LS	+ nonarticulated	–
Croton sp.	Brazil: Harley et al. 25226 (K)	LS, E	+ nonarticulated	–
Croton sp.	Brazil: Harley et al. 24986 (K)	LS	+ nonarticulated	–
Cyrtogonone argentea Prain	K: Thomas 4738	L	+ nonarticulated (stem only)	+

TABLE 1. Continued.

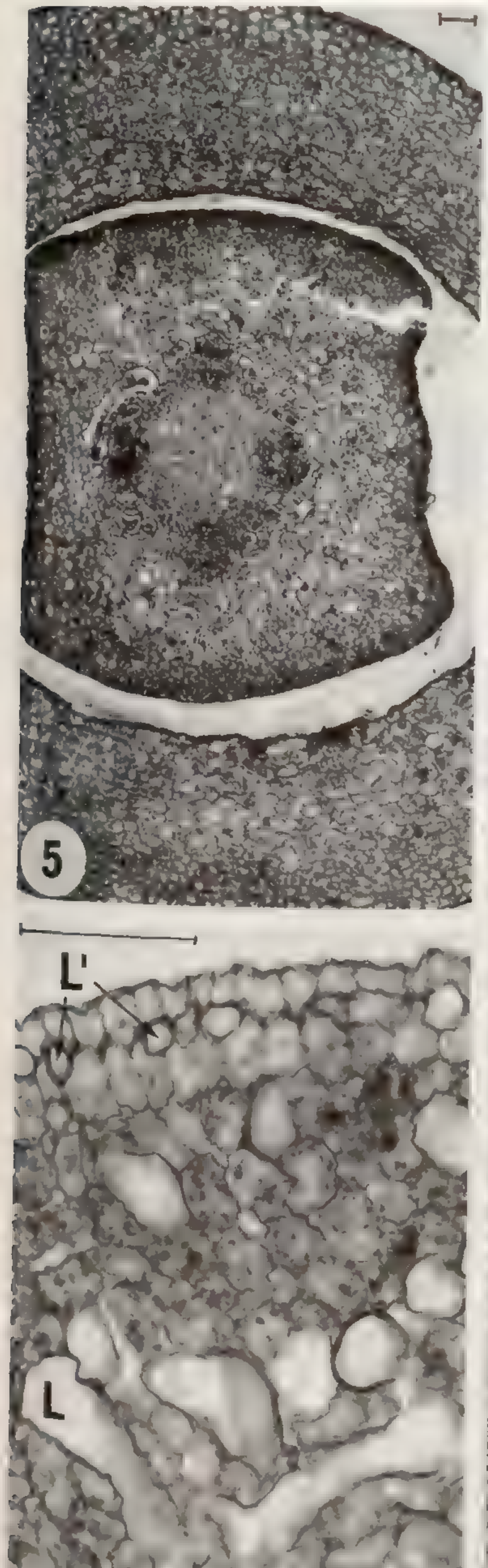
Taxon	Source & data[a]	Plant part[b]	Laticifers[c]	Sclereids in leaves[c]
Garcia nutans Rohr	K: Gillis 15070	L	+ nonarticulated	–
Grossera vegenei Pax	K: Bamps 2363	L	–	+
Hevea confusa Hemsl.	SC: cult. Castleton Gdns.	E	+ articulated	–
Jatropha curcas L.	HK (no data)	LS, E	+ nonarticulated	–
Manihot sp. aff. *caerulescens* Pohl.	Brazil: Harley et al. 25098 (K)	LS	+ articulated	–
Micrandra elata Muell. Arg.	K: Lindeman et al. 256	L	+ nonarticulated	–
Micrandra minor Benth.	K: Schultes & Lopez 8959	L	+ nonarticulated	–
Micrandra siphonoides Benth.	K: Schultes & Lopez 10180	L	+ nonarticulated	–
Micrandra prucei (Muell. Arg.) Schultes	K: Schultes & Pires 9057	L	+ nonarticulated	–
Neoboutonia macrocalyx Pax	K: Lewalle 8000	L	+ nonarticulated	–
Pausandra macropetala Ducke	K: Ducke 7148	L	+ nonarticulated (petiole only)	+
Ricinocarpus ledifolius F. Muell.	K: Coveney 6842	L	+ nonarticulated	
Ricinocarpus pinifolius Desf.	K: Coveney 7253	L	+ nonarticulated	
Ricinodendron heudolotii (Baill.) Pierre ex Hecke	K: Troupin 3450	L	+ nonarticulated	–
Spirostachys venenifera (Pax) Pax	K: Kisena 342	L	+ nonarticulated	–
Trigonostemon chinensis Merrill	K: Thow 78487	L	–	+
Vernicia cordata (Thunb.) Airy Shaw	K: s.n. (cult. Grossens)	L	+ nonarticulated	–
Euphorbioideae				
Euphorbia lathyris L.	HK: Aronson s.n.	E	+ nonarticulated	–
Synadenium grantii Hook.	HK: Brandham et al. 2549	E	+ nonarticulated	–

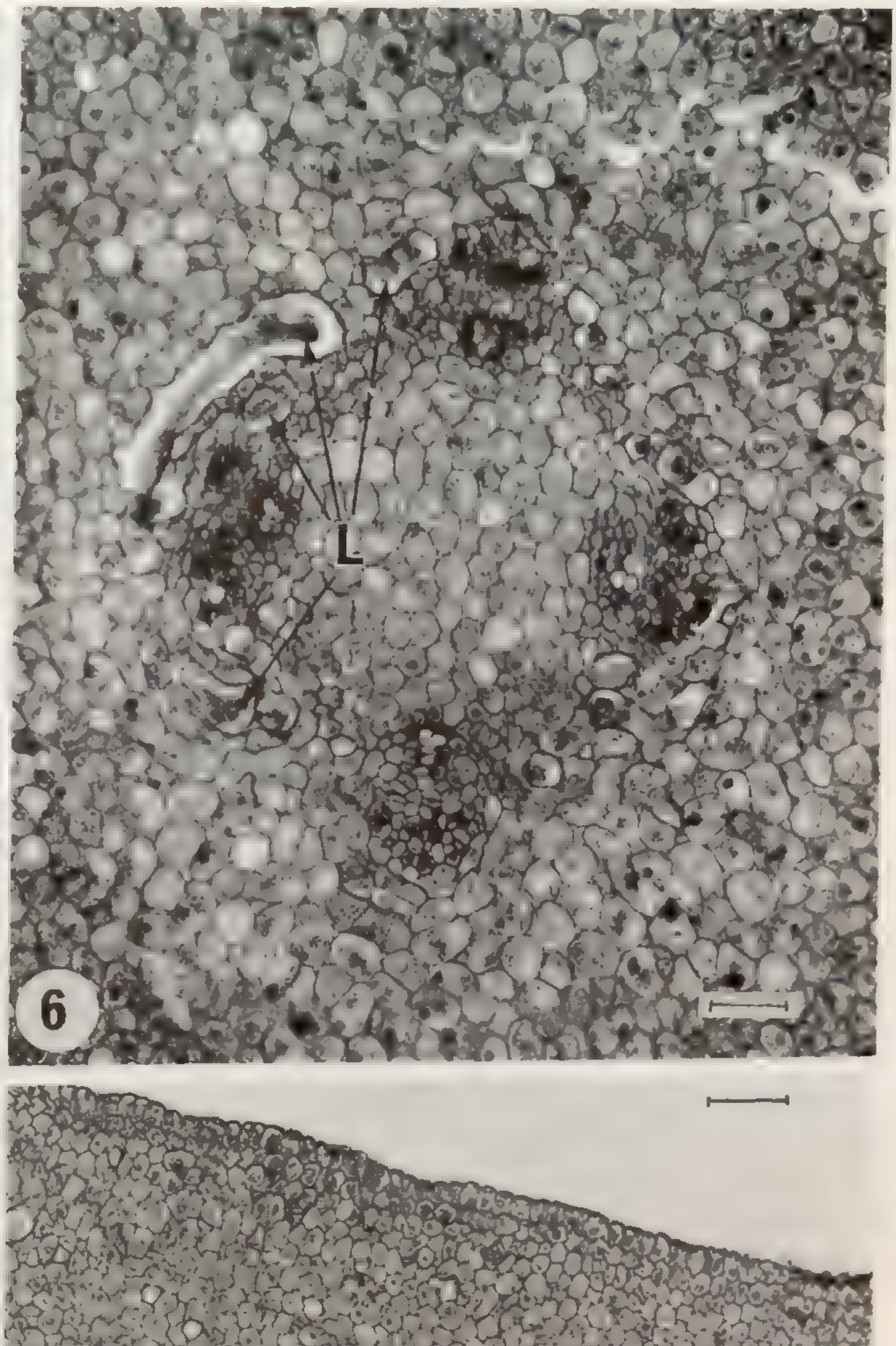
[a] STRI = Smithsonian Tropical Research Institute; B.G. = Botanic Garden; K = herbarium of the Royal Botanic Gardens, Kew; HK = living collections at Kew; Z = herbarium of the Institut für Systematische Botanik, Zürich; SC = Kew spirit collection.
[b] E = seeds for embryo extraction; L = leaves; S = stems.
[c] + = present; – = absent.

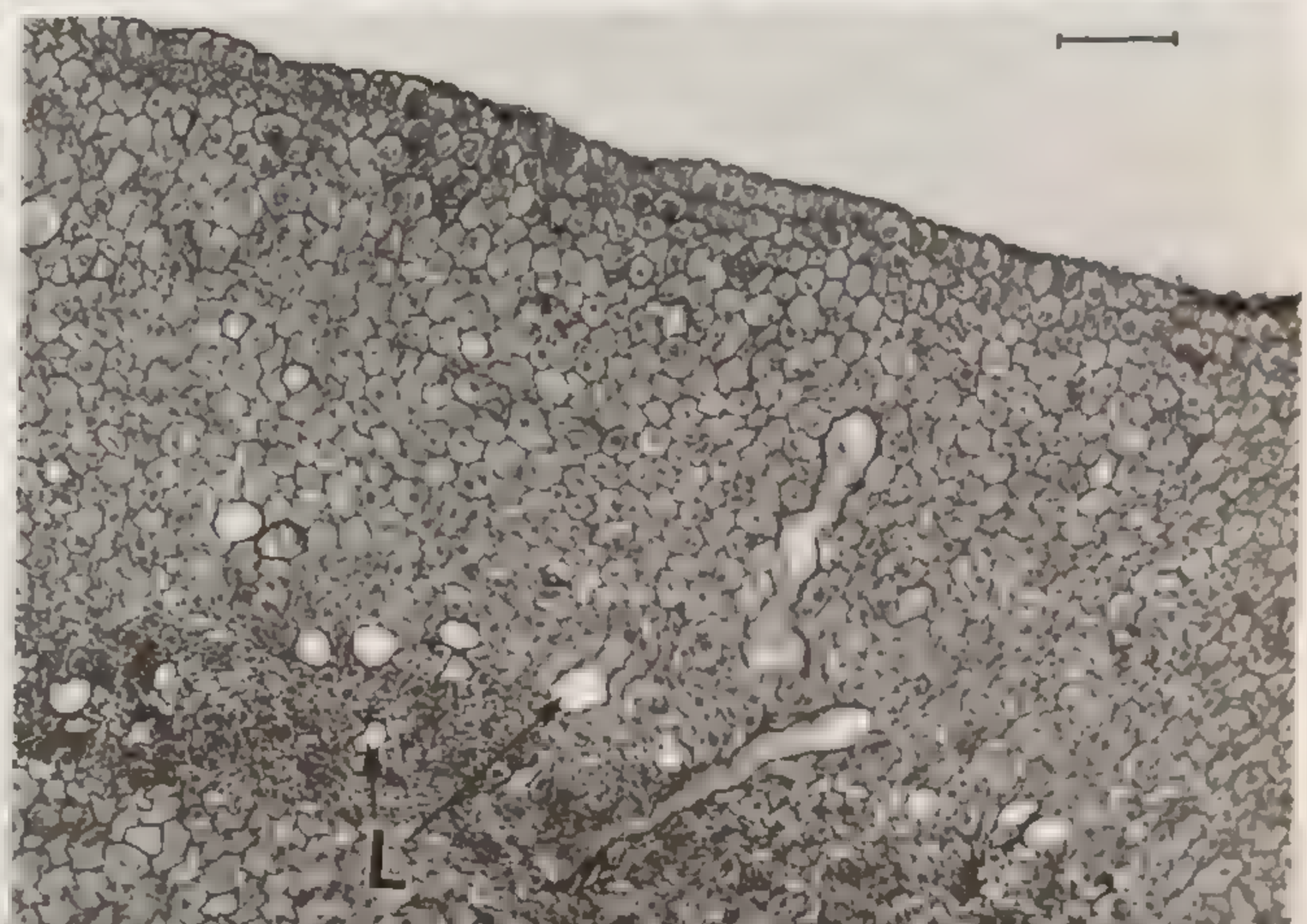


FIGURES 1–4.[3] Embryos of *Baloghia lucida*.—1. Longitudinal section through apex (A). Laticifer (L) branching toward subepidermal ring.—2. Cross section through hypocotyl, with laticifers (L) toward periphery of vascular tissue.—3. Detail of cross section through hypocotyl.—4. Cross section of cotyledons. L = laticifer. Scale bars = 50 μm.

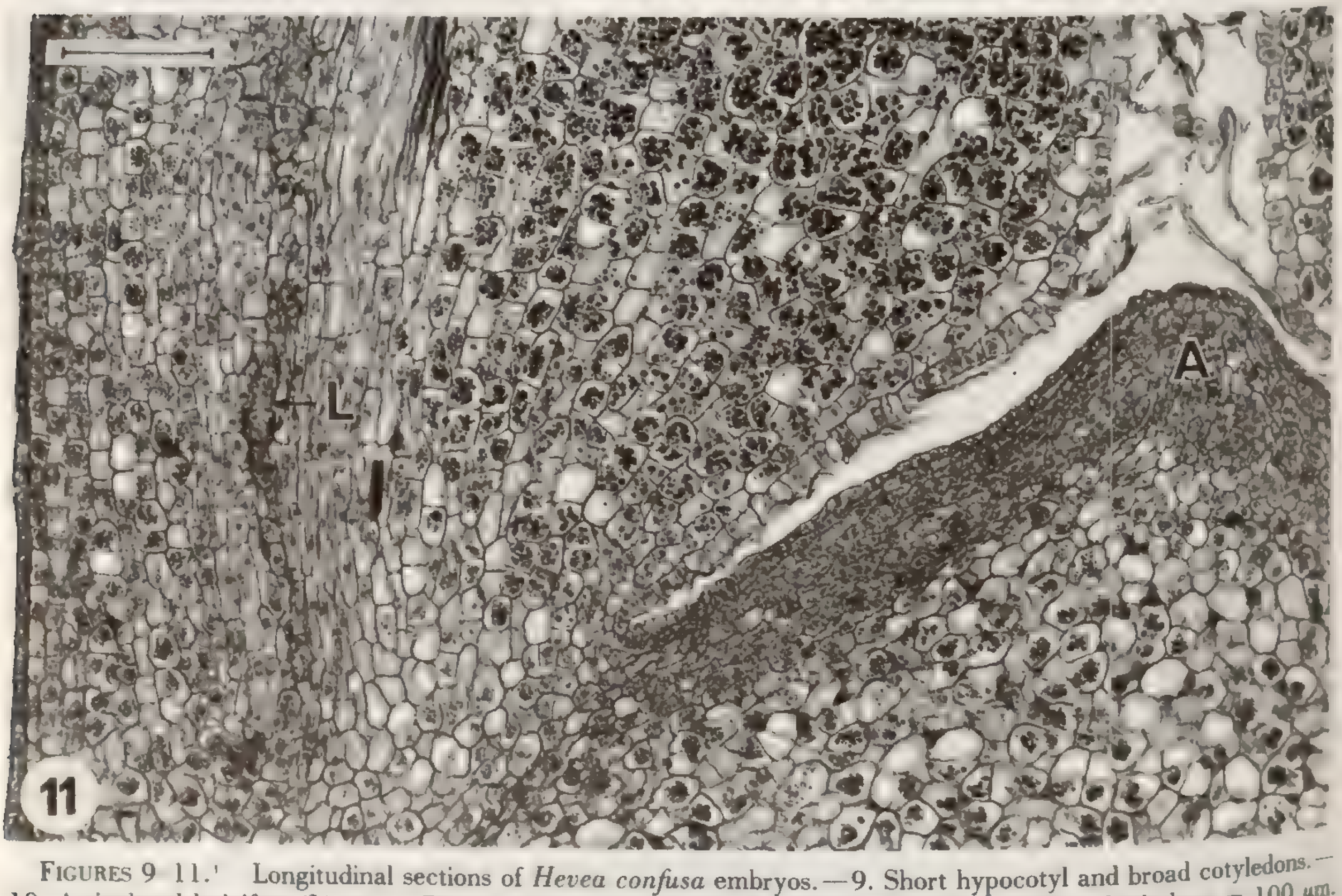
[3] Voucher or source information is in Table 1, unless given in the caption.







FIGURES 5–8. Cross sections of embryo hypocotyls.—5, 6. *Synadenium grantii*. Laticifer initials and branches (L) around outer edge of vascular tissue. Generally a single initial is present on each side of each of four vascular bundles, forming ca. eight initials, which then ramify.—7. *Euphorbia latifolia*. Distinct subepidermal ring of laticifers (L') and inner ramifying laticifers (L).—8. *Aleurites triloba*. Laticifer initials (L) in vascular tissue. Scale bars = 50 μm.



FIGURES 9–11. Longitudinal sections of *Hevea confusa* embryos.—9. Short hypocotyl and broad cotyledons.—10. Articulated laticifers (L).—11. Region near apex (A), showing laticifers (L) in cotyledon. Scale bars = 100 μm.

(Fig. 10) are present in the outer part of the provascular tissue (i.e., the protophloem region, as with nonarticulated laticifers of other genera) of the cotyledonary node and in the base of the cotyledons (Fig. 11). The cotyledonary initials are the most well developed at this stage, as Scott (1886) also found in *Hevea brasiliensis*. Intrusive growth is not pronounced, although some short branches are present. Later articulated laticifers form elongated intrusive branches between surrounding cells in the same way as nonarticulated laticifers, especially in the leaf mesophyll (Rudall, 1987).

LEAVES AND STEMS

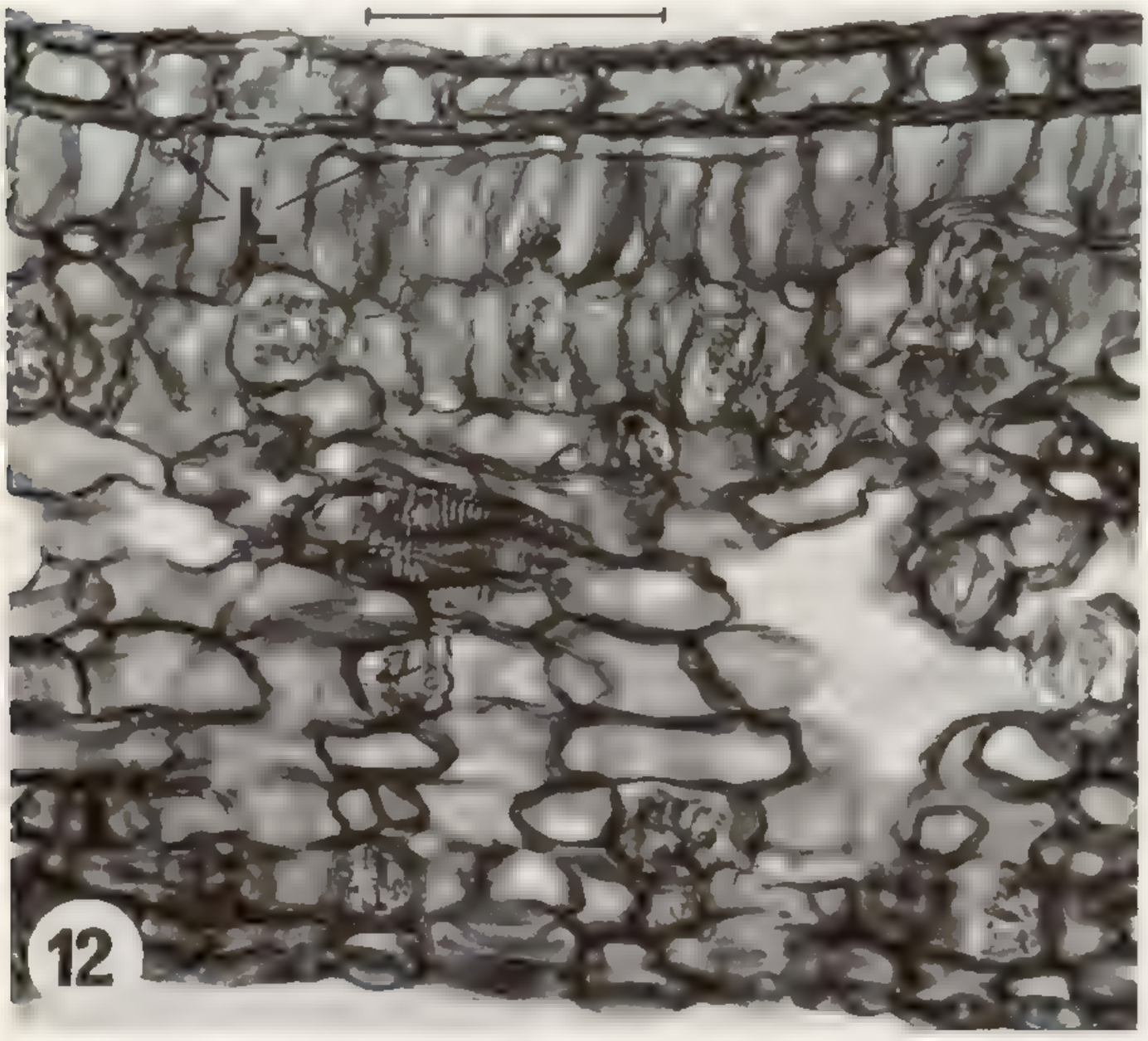
Acalyphoideae. *Omphalea*, which exudes a clear latex that becomes red on oxidation, has abundant nonarticulated laticifers in the leaf mesophyll and stem. Laticifers were also observed in the tissue above extra-floral nectaries on the abaxial leaf surface. In *Mallotus subulatus*, although laticifers are absent in mature leaves, many narrow intrusive thick-walled sclereid branches are present.

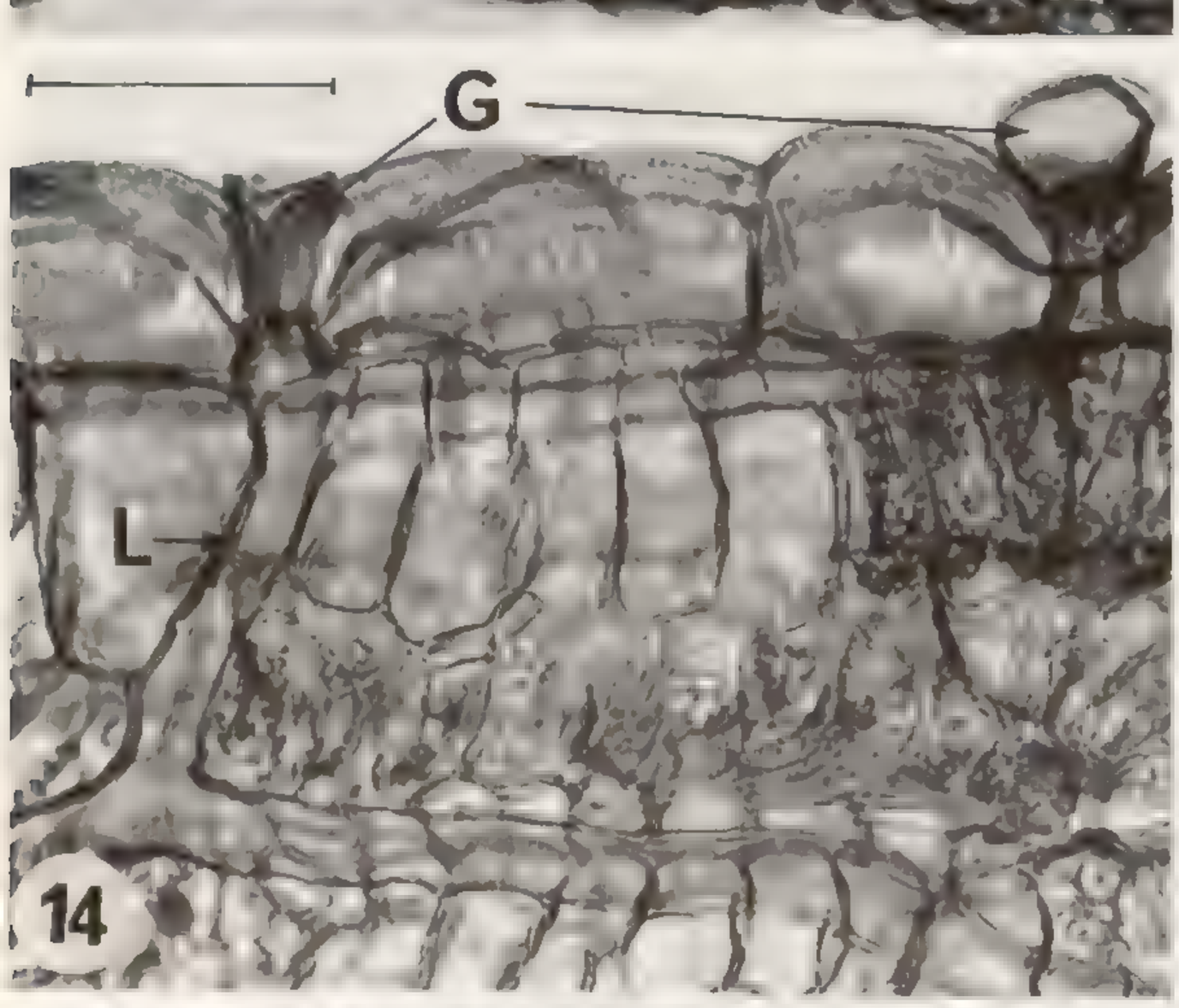
Crotonoideae. Thin-walled laticifers were observed here in most Crotonoideae examined (Table 1): *Adenocline acuta*, *Baloghia lucida*, *Bertya mitchellii*, *Beyeria leschenaultii*, *Codiaeum variegatum* (Figs. 15, 16), *Croton* spp. (Figs. 13, 17–19), *Cyrtogonone argentea* (stem only), *Garcia nutans* (Fig. 12), *Jatropha curcas* (Fig. 20), *Micrandra* spp., *Neoboutonia macrocalyx*, *Pausandra macropetala* (petiole only), *Ricinodendron heudelotii*, *Spirostachys venenifera*, and *Vernicia caudata*. Thick-walled sclereids were observed in leaves of *Grossera veginei* and *Trigonostemon chinensis* (Fig. 22) (in the latter sometimes protruding between epidermal cells or to hair bases). Pax (1884) recorded laticifers in *Trigonostemon*; furthermore, in our material of *Cyrtogonone argentea*, laticifers are present in the stem phloem, cortex, and pith, but only thick-walled sclereids in the leaves, indicating that the "sclereids" in these cases may be thick-walled laticifers. Similarly, in *Pausandra macropetala* laticifers were observed in the petiole, but only thick-walled sclereids in the mesophyll. In *Codiaeum variegatum*, sclereids were present in older leaves, but absent in younger, as Rao & Tewari (1960) also reported. In *Codiaeum variegatum*, where laticifers frequently intrude between epidermal cells, as in *Baloghia lucida* (Rudall, 1987), the fact that laticifers are continuously growing is demonstrated by the presence of many more points of laticifer intrusion in epidermises of older leaves than young leaves (Figs. 15, 16). In some species latex is recorded only in young tissues (e.g., in *Glycydendron*, Roosmalen, 1985), and laticifers presumably cease to function (probably becoming thick-walled; see below). The distinction between the two cell types in these taxa is therefore not always clear; "laticifers" in young leaves may become "sclereids" in older ones. In the literature such cells (with intrusive branches) are termed laticifers if they are thin-walled, and sclereids if they are thick-walled.

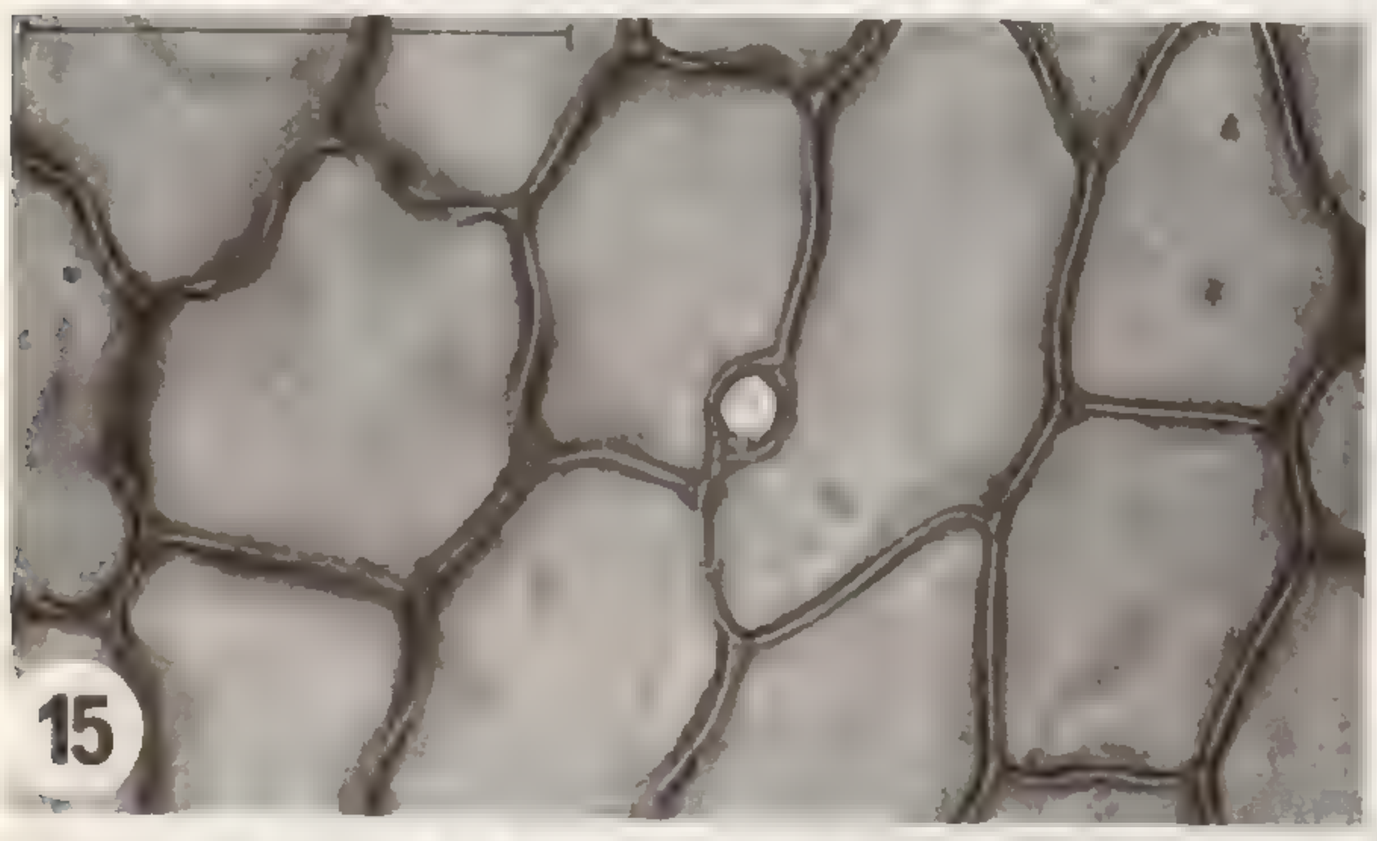
Occasional cross-walls were observed in leaf laticifers of *Micrandra elata*, as other workers have also occasionally reported in other genera (e.g., de Bary, 1884, in *Euphorbia lathyris*; Dehgan & Craig, 1978, in *Jatropha* spp.). Otherwise laticifer structure is essentially similar in all genera concerned (apart from the articulated forms occurring in *Hevea*, *Manihot*, and *Cnidoscolus*), the main differences being in size and quantity. In Crotonoideae laticifers generally occur in the phloem of the stem, petiole, and midrib bundles, and may be large and easily distinguishable in cross section (Fig. 18), or sometimes smaller (Fig. 19). Laticifers in the leaf mesophyll range in size from narrow (Fig. 12) to broader than neighboring mesophyll cells. In several species laticifers extend either directly to the plant surface (e.g., in *Codiaeum variegatum*, Figs. 15, 16) or into the bases of trichomes (e.g., *Croton* spp., Fig. 13). In *Beyeria* and *Ricinocarpus*, laticifers were occasionally observed in direct contact with small glandular hairs on the plant surface (Fig. 14). In many cases (e.g., *Codiaeum variegatum*), the narrowest laticifers, immediately within the epidermis, are the most highly branched.

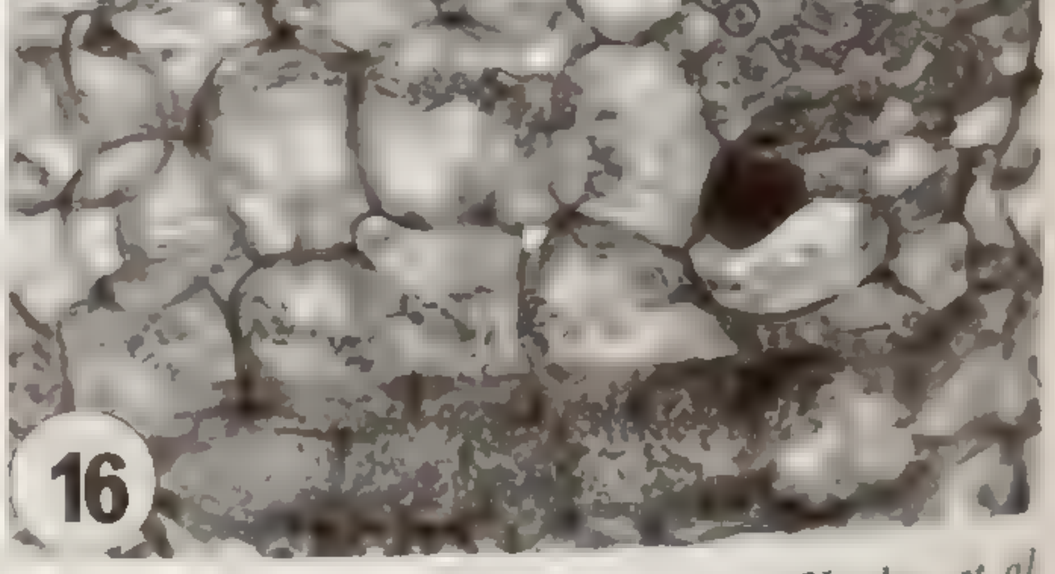
A wide variation of nonarticulated laticifers is displayed by various species of *Croton*. Most species have abundant nonarticulated laticifers, though sometimes less frequent in older stems (e.g., in *C. comosus*). Distribution ranges from extremely abundant and highly branched in all aerial tissues (e.g., *C. conduplicatus*, Fig. 19) to (rarely) apparently absent. Other authors, such as McPherson & Tirel (1987), have reported latex apparently absent in some species of *Croton*, and this variation may well have some taxonomic significance within the genus. However, species that lack laticifers may have the capacity to develop them under certain environmental conditions, or at particular stages in their life cycle, and a better understanding of the function of latex in different species would be necessary to establish this.

In this investigation, typical articulated laticifers were observed in stems of *Manihot* sp. aff. *caerulescens* (Fig. 21) and *Hevea confusa* embryos (Figs. 9–11). In *Manihot*, *Hevea*, and *Cnidoscolus*, which have articulated laticifers in the stems, transitional nonarticulated (intrusively branched) forms are also present, particularly in the leaves (Rudall, 1987). Articulated laticifers (recorded in *Hevea*, *Manihot*, and *Cnidoscolus*: Rudall, 1987) are continuously produced in the developing primary phloem, and also in the vascular cambium. However, in *Croton conduplicatus* occasional (rare) instances were observed of ray initials in the vascular cambium intruding between adjacent phloem ray cells in the manner of young laticifer initials (Rudall, 1989), i.e., new laticifer initials forming in the vascular cambium. Since no evidence of cell fusion was

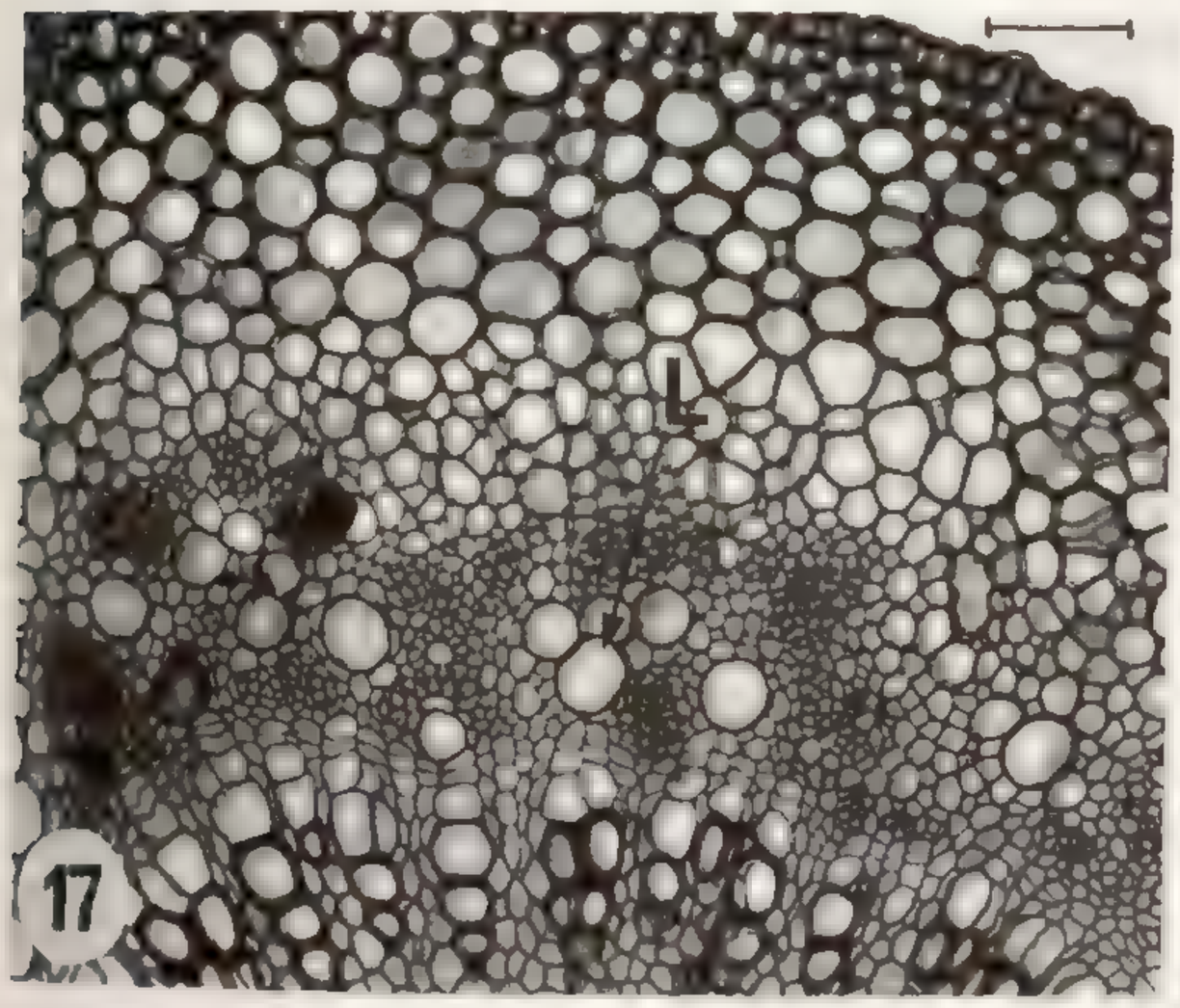


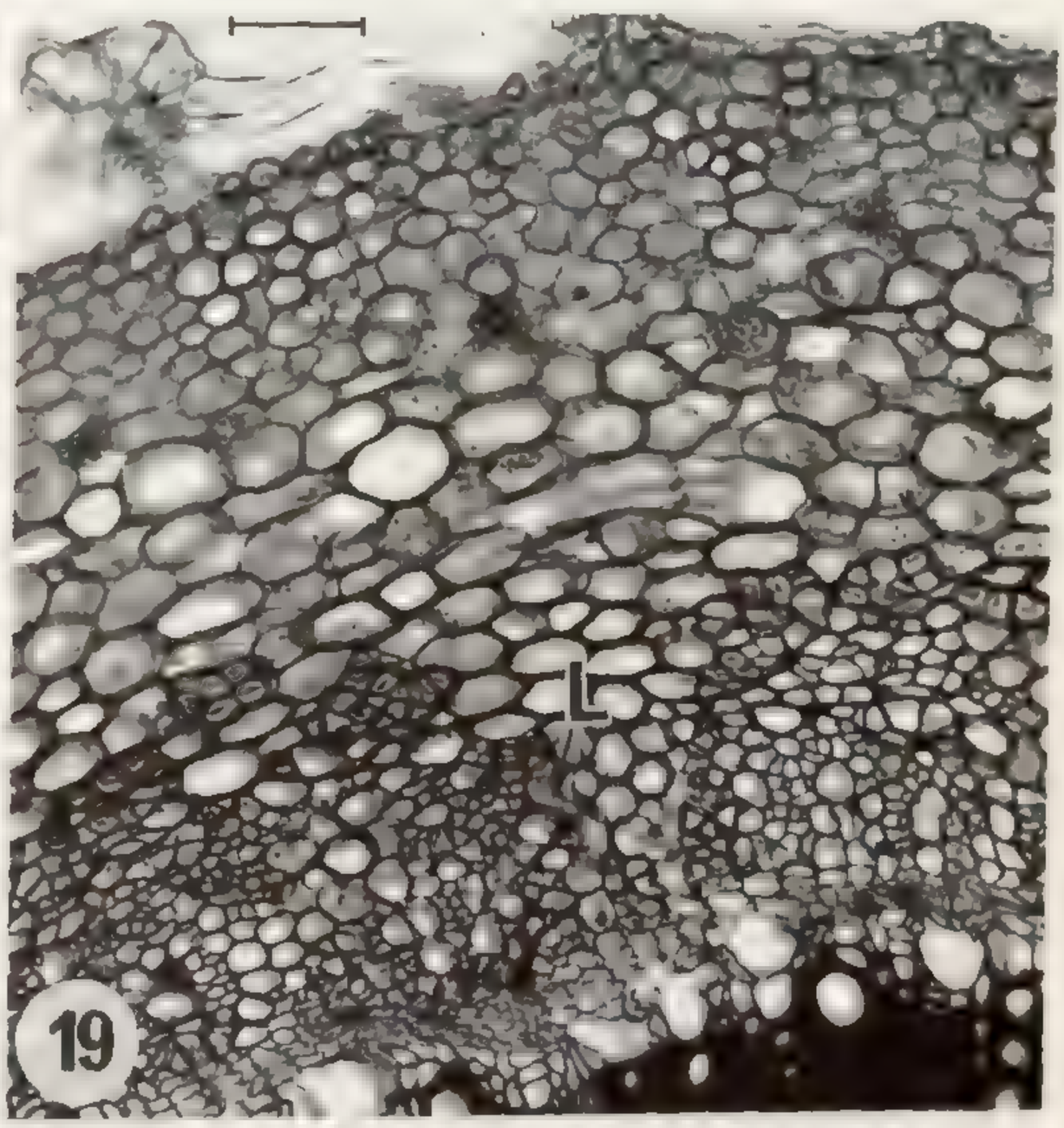


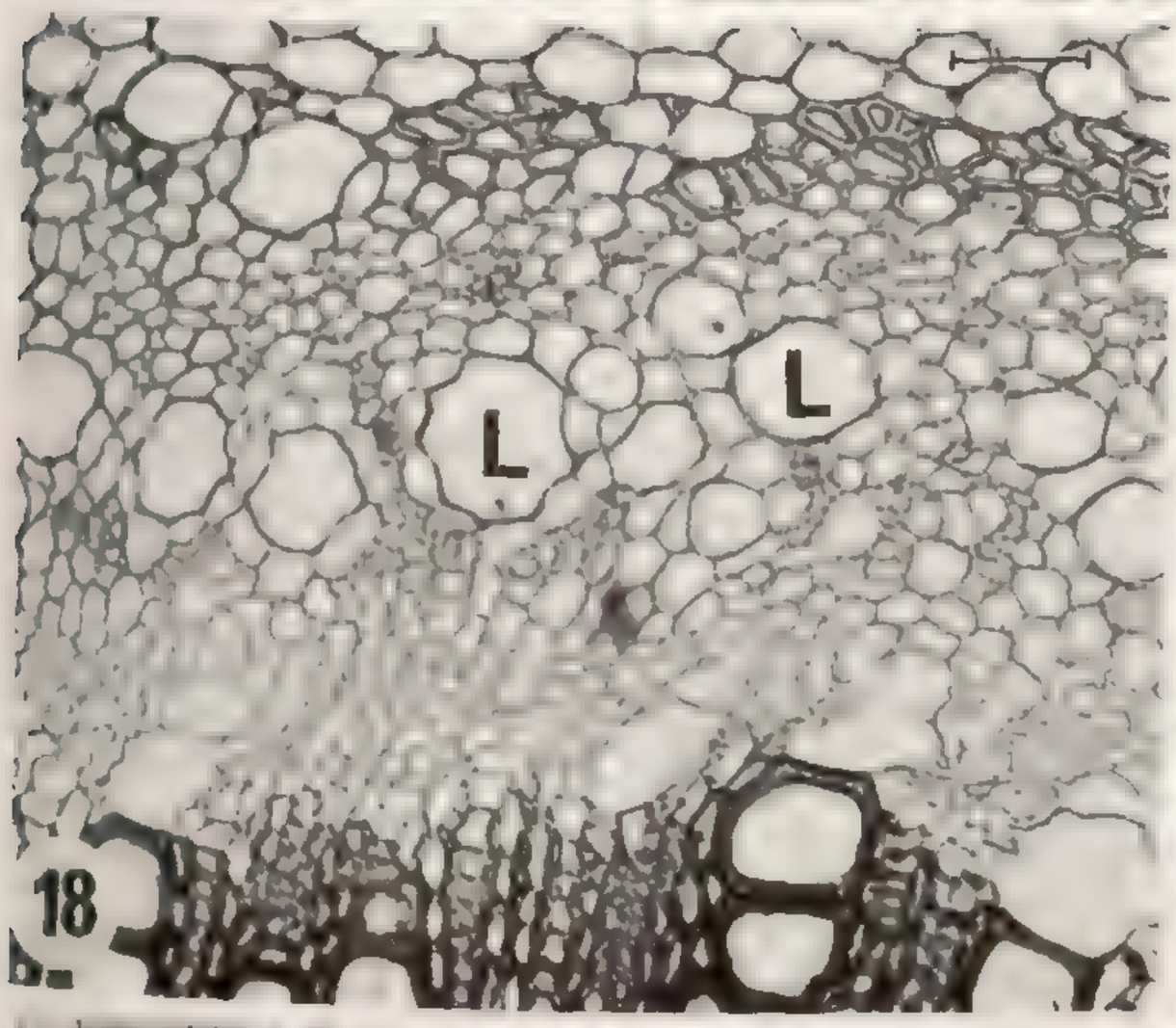


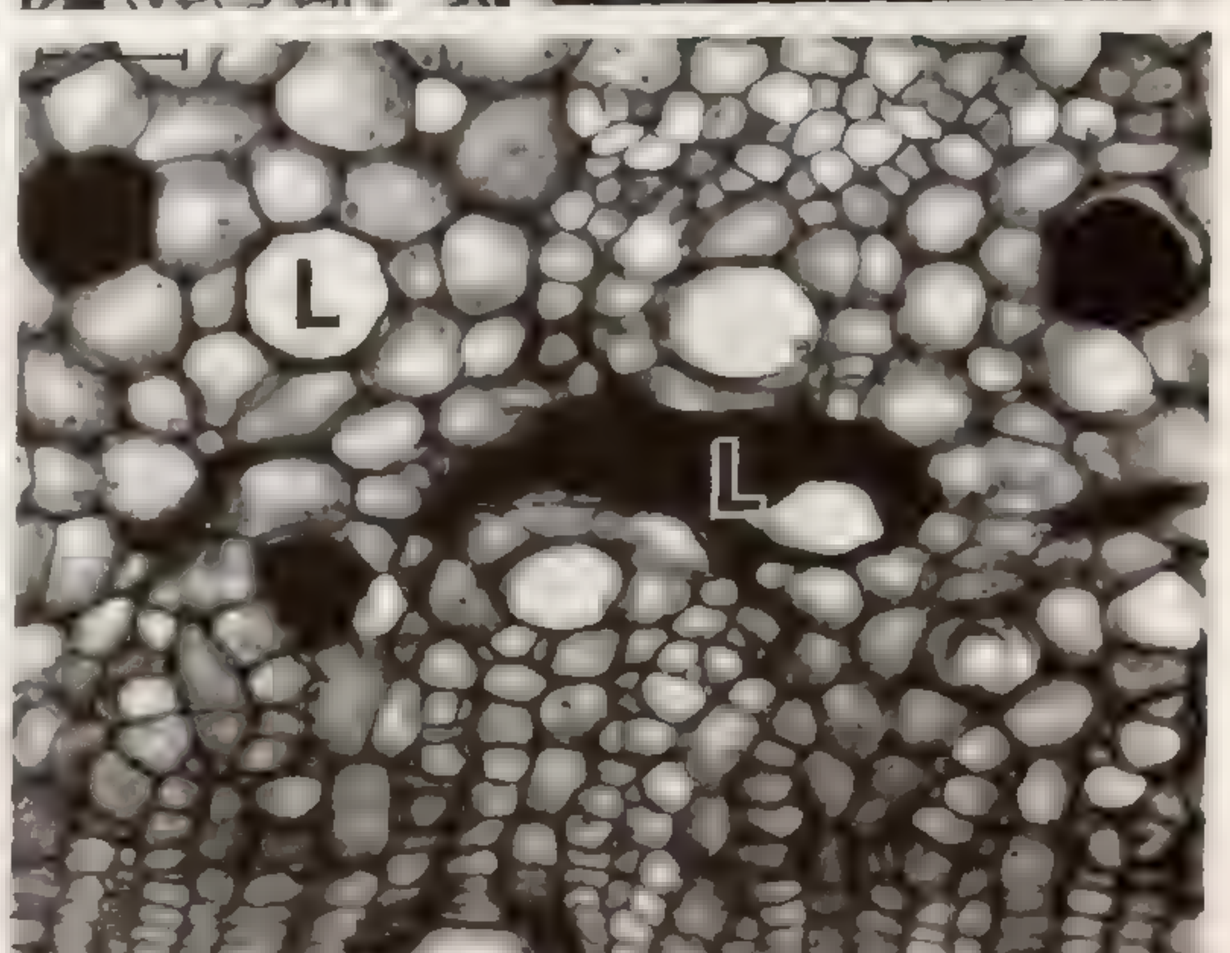


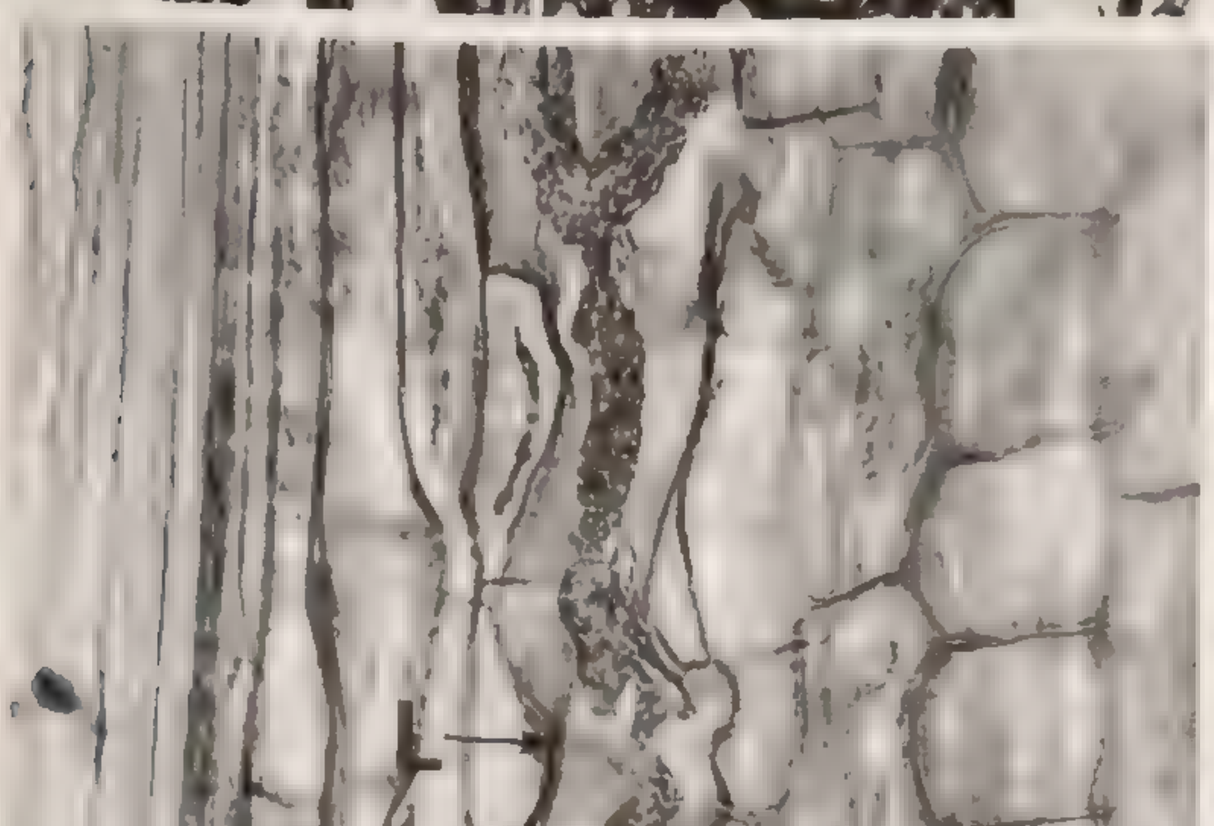
FIGURES 12–16.[1] Laticifers (L) in leaves.—12. *Garcia nutans*, cross section.—13. *Croton* sp. (*Harley et al. 24986*), laticifers branching into base of stellate hair, with glandular region (G).—14. *Beyeria leschenaultii*, cross section. Laticifers extending to bases of glandular hairs (G). 15, 16. *Codiaeum variegatum*.—15. Leaf surface, showing point of intrusion of laticifer between epidermal cells.—16. Cross section, with laticifers intruding between epidermal cells. Scale bars = 50 μm.

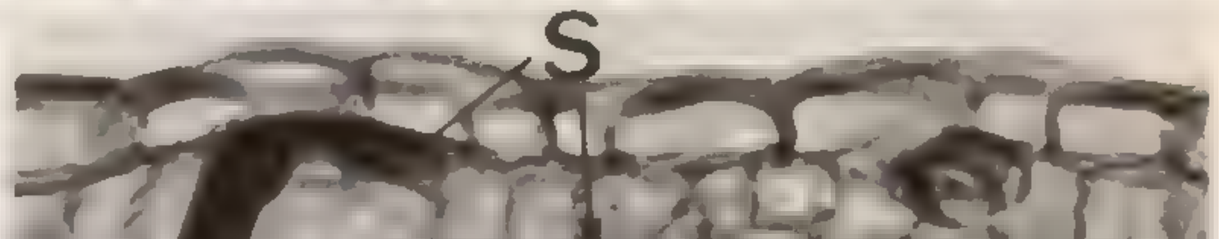












FIGURES 17–22.[3] 17, 18. *Croton* sp. (*Harley et al. 24843*).—17. Midrib, cross section.—18. Stem, cross section.—19. *Croton conduplicatus*, stem cross section.—20. *Jatropha curcas*, stem cross section.—21. *Manihot* sp., longitudinal section of stem, phloem region, showing laticifer.—22. *Trigonostemon chinensis*, leaf cross section, showing sclereids (S). Scale bars = 50 μm. L = laticifer.

found, these are nonarticulated laticifers. This species is unusual in the abundance of its laticifers and their degree of branching, and it is therefore possible that this apparently very unusual phenomenon is simply more detectable in this material, because new laticifers produced in the vascular cambium begin to branch immediately, rather than elongating for a period. A "secondary" laticifer (formed from the vascular cambium) that elongated in the region close to the vascular cambium would be virtually indistinguishable from a "primary" laticifer (formed in primary tissues) that extended into this region from the cortex; indeed many species have abundant laticifers in the most recently formed secondary phloem, and their origin is difficult to determine.

Discussion

LATICIFER EVOLUTION

The traditional difference between the articulated and nonarticulated types of laticifer is that the former are multicellular and the latter unicellular. Typical articulated laticifers are often easily recognizable by their eccentrically convoluted appearance (Fig. 21). Nevertheless, as de Bary (1884) and other early workers have also observed, there are several similarities and transitional forms that tend to narrow the gap between the extremes of both categories: (1) In Crotonoideae nonarticulated laticifers originate in the protophloem of the embryo, and (as Gaucher, 1902, also noted) in general predominate in the phloem of older tissues, in common with articulated laticifers of other crotonoid genera, and in contrast to the condition of Euphorbioideae. (2) Single cell members of articulated laticifers in leaves of, e.g., *Hevea* grow intrusively between mesophyll cells, in the same manner as nonarticulated laticifers (Rudall, 1987). Boblioff (1923) observed these intrusive "amoeboid" forms both in leaves and the inner integument of the seed of *Hevea*. Other anomalous cell types have also been reported by several early workers; for example, Pax mentioned that in *Joannesia*, *Garcia*, and *Aleurites* (all Crotonoideae), certain "closed sacs" grow to a great length. The "articulated laticifers" that Dehgan & Craig (1978) described in *Jatropha* are very different from those of *Hevea*, *Cnidoscolus*, and *Manihot*, but may represent another form. (3) Nonarticulated (i.e., intrusive, unicellular) laticifers, although normally primary in origin, have also been observed in *Croton* to originate in secondary tissue derived from the vascular cambium (Rudall, 1989), a type of development usually associated only with articulated laticifers.

Scott (1886) believed, following Pax (1884), that articulated and nonarticulated laticifers evolved separately, both from secretory sacs; in fact, rows of large parenchymatous cells with dark contents frequently occur in the phloem of species without latex, such as *Androstachys johnsonii* and *Malotus subulatus*. Furthermore, occasional crosswalls have been reported in nonarticulated laticifers of several species, such as *Micrandra elata*. However, an alternative theory, probably more plausible in view of the similarities demonstrated here between the two laticifer types, is that articulated laticifers of *Hevea*, *Cnidoscolus*, and *Manihot*, and the transitional forms of other genera represent more recent developments from the nonarticulated type (although further data are essential, particularly on laticifer ontogeny). The nonarticulated type is by far the most common type among Euphorbiaceae, and indeed other dicotyledons, and is therefore probably the plesiomorphic type in this family.

LATICIFERS AND SCLEREIDS

Elongated "fiberlike," occasionally branched sclereids occur in mesophyll of leaves of many euphorbiaceous genera, generally (though not exclusively) where laticifers are absent. In view of the apparent relationship between the two cell types (see below and Observations, above), this near-exclusivity is consistent with a probable homology between them, although this hypothesis requires further testing. Metcalfe & Chalk (1950) and Rao & Das (1979) recorded sclereids in several genera, especially among Acalyphoideae, such as *Acalypha* and *Chaetocarpus*. *Androstachys johnsonii* (Oldfieldioideae), which lacks latex, has copious highly branched gelatinous sclereids in the mature leaves, similar to laticifers in many respects, associated with the epidermis and veins, and often also with the bases of probable water-absorbing trichomes (Alvin, 1987). Among Crotonoideae, several genera (e.g., *Grossera*, *Pausandra*, and *Trigonostemon*) have sclereids instead of laticifers in the leaves, although stems have not been investigated in these cases: *Cyrtogonone argentea* has thin-walled laticifers in the stem, but only sclereids in the leaves. In all cases the sclereids resemble laticifers in structure and distribution, both cell types being extremely elongated and associated with vascular tissue and epidermis; they are not easily distinguishable in sections, except in terms of wall thickness. Moreover, thick-walled laticifers are not uncommon (e.g., in stems of *Euphorbia abdelkuri*; Rudall, 1987). Rao & Tewari (1960)

reported that in *Codiaeum variegatum*, laticifers in young leaves actually become sclereids in older leaves; indeed in our material of this species sclereids were present in older leaves, and absent in younger.

SYSTEMATIC AND PHYLOGENETIC CONSIDERATIONS

Many plants are known to produce latex, but the capacity for latex production does not in itself necessarily imply relationship. Latex-producing dicotyledon families, such as Apocynaceae, Asclepiadaceae, Eucommiaceae, Sapotaceae, and Moraceae, are widely distributed throughout various dicotyledon orders. Nevertheless, as many authors (e.g., Mahlberg & Sabharwal, 1968) have also observed, there is remarkable similarity in laticifer morphology and development between comparatively unrelated dicotyledons, especially considering the anomalous nature of the cell types concerned. The apparent relationship between laticifers and branched sclereids (astrosclereids) is not restricted to Euphorbiaceae; in other families the two cell types are often mutually exclusive in related genera, also indicative of a possible homology between them. A survey of dicotyledon families in this respect, though inappropriate here, might shed further light on the subject and help to indicate affinities of Euphorbiaceae. Sister-group relationships of Euphorbiaceae have been much disputed, but probably exist among the Malvales, Geraniales, or Linales (Webster, 1987a, b). Although sclereids occur widely among these orders, there are very few latex-producing families; therefore, in the absence of a latex-producing sister group, and if Euphorbiaceae is indeed monophyletic, the most likely inference is that latex production evolved de novo within the family.

Within Euphorbiaceae, Webster (1987b) postulated that Crotonoideae and Euphorbioideae (latex and laticifers usually present) evolved independently from Acalyphoideae (latex and laticifers rarely present). Subfamilies Oldfieldioideae and Phyllanthoideae (latex and laticifers absent) are closely linked to each other. Thus there are three main divisions within Euphorbiaceae on the basis of latex and other characters: Oldfieldioideae/Phyllanthoideae, Acalyphoideae, and Crotonoideae/Euphorbioideae. However, Acalyphoideae divides into two groups: without latex (most genera) and with latex (e.g., *Macaranga*, *Omphalea*). If (as seems most likely) latex production evolved within Euphorbiaceae (in the Euphorbioideae/Crotonoideae lineage), the abundant presence of laticifers in *Omphalea* casts doubt on its systematic position in Acalyphoideae. Variation in this character in Acalyphoideae (also in a few Crotonoideae) indicates paraphyly, although it is also possible that a reversal (i.e., loss of latex) may yet be demonstrated on the basis of congruence in other characters.

LITERATURE CITED

ALVIN, K. L. 1987. Leaf anatomy of *Androstachys johnsonii* Prain and its functional significance. Ann. Bot. 59: 579–591.

BARY, A. DE. 1884. Comparative Anatomy of the Vegetative Organs of the Phanerogams and Ferns. [English translation.] Clarendon Press, Oxford.

BOBLIOFF, W. 1923. Anatomy of *Hevea brasiliensis*. Zurich.

CHAUVEAUD, M. L. G. 1891. Recherches embryogéniques sur l'appareil laticifère des Euphorbiacées, Urticacées, Apocynées et Asclépiadées. Ann. Sci. Nat., Botanique 14(1–2): 1–160.

DEHGAN, B. & M. E. CRAIG. 1978. Types of laticifers and crystals in *Jatropha* and their taxonomic implications. Amer. J. Bot. 65: 435–352.

GAUCHER, L. 1902. Recherches anatomiques sur les Euphorbiacées. Ann. Sci. Nat., Botanique 15(1): 161–309.

MAHLBERG, P. G. & P. S. SABHARWAL. 1968. Origin and early development of non-articulated laticifers in embryos of *Euphorbia marginata*. Amer. J. Bot. 55: 375–381.

———, D. G. DAVIS, D. S. GALITZ & G. D. MANNERS. 1987. Laticifers and the classification of *Euphorbia*: The chemotaxonomy of *Euphorbia esula* L. Bot. J. Linn. Soc. 94: 165–180.

MCPHERSON, G. & C. TIREL. 1987. Flore de la Nouvelle Calédonie et dépendences. Euphorbiaceae I. Mus. d'Hist. Nat., Paris.

METCALFE, C. R. 1967. Distribution of latex in the plant kingdom. Econ. Bot. 21: 115–127.

——— & L. CHALK. 1950. Anatomy of the Dicotyledons. Clarendon Press, Oxford.

PAX, F. 1884. Die Anatomie der Euphorbiaceae in ihrer Beziehung zum System Derselben. Bot. Jahrb. 5: 384–421.

RAO, A. R. & J. P. TEWARI. 1960. On the morphology and ontogeny of the foliar sclereids of *Codiaeum variegatum* Blume. Proc. Nat. Inst. Sci. India. 26B: 1–6.

RAO, A. T. & S. DAS. 1979. Leaf sclereids—Occurrence and distribution in the angiosperms. Bot. Not. 132: 319–324.

ROOSMALEN, M. G. M. VAN. 1985. Fruits of the Guianan Flora. Inst. Syst. Bot., Utrecht University.

RUDALL, P. J. 1987. Laticifers in Euphorbiaceae—A conspectus. Bot. J. Linn. Soc. 94: 143–163.

———. 1989. Laticifers in vascular cambium and wood of *Croton* spp. (Euphorbiaceae). IAWA Bull. n.s. 10: 379–383.

SCHAEFFER, J. 1971. A revision of *Endospermum* Benth. (Euphorbiaceae). Blumea 19: 171–192.

SCHMALHAUSEN, J. 1877. Beiträge zur Kenntnis das Milchsaftbehälter der Pflanzen. Mém. Acad. Imp. Sci. St. Petersburg. Ser. 7 24: 1–27.

SCOTT, D. H. 1884a. On the laticiferous tissue of *Manihot glaziovii* (the Ceara rubber). Quart. J. Microsp. Sci. 24: 193–203.

———. 1884b. Note on the laticiferous tissue of *Hevea spruceana*. Quart. J. Microsp. Sci. 24: 204–206.

———. 1886. On the occurrence of articulated laticiferous vessels in *Hevea*. J. Linn. Soc. (Bot.) 21: 566–573.

Spix, J. B. & C. F. P. Martius. 1828. Pp. 612, 726 *in* Reise in Brasilien. M. Lindauer, München.

Webster, G. L. 1975. Conspectus of a new classification of the Euphorbiaceae. Taxon 24: 593–601.

———. 1987a. The saga of the spurges: A review of classification and relationships in the Euphorbiales. Bot. J. Linn. Soc. 94: 3–46.

———. 1987b. Evolution and distributional history of the Euphorbiaceae. Abstracts, XIV International Botanical Congress, Berlin (West) Germany.

THE RELATIONSHIPS OF THE EUPHORBIEAE (EUPHORBIACEAE)[1]

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ABSTRACT

The Euphorbieae and Hippomaneae, though both usually placed in subfamily Euphorbioideae, differ in many inflorescence details and can be linked unambiguously only by one cryptic character: the rod-shaped starch grains in the latex. While the Hippomaneae have inflorescences very similar to those of many other members of the Euphorbiaceae, the Euphorbieae have an inflorescence so specialized that one seems to be forced to relate it to other members of the family through a hypothetical ancestor with a synflorescence of axillary bisexual cymes more primitive than most extant taxa possibly other than *Jatropha*.

A primary aim of this symposium is to review critically Webster's (1994) classification of the Euphorbiaceae. This paper is an attempt to share a speculation arising from misgivings over the supposed homogeneity of the subfamily Euphorbioideae. This is not a presentation of the results of prolonged and detailed research but rather speculations arising while producing a routine Flora account of the Euphorbiaceae for the *Flora of Ethiopia* (31 genera, 209 species), coupled with a long-standing interest in *Euphorbia* (the largest genus within the Ethiopian flora), particularly the succulent species. A Flora writer should delve into the larger scale taxonomy of those families that must be covered, but is rarely allowed the time to carry out anything more than superficial investigations on taxa not actually included in the Flora. Thus the following ideas must not be regarded as anything more than simple-minded speculations.

Determining the relationships of a group as specialized as the Euphorbieae used to be of little concern to a Flora writer. The matter became a little more relevant with the advent of cladistics, where the methodology demands a working hypothesis of probable sister groups and character polarization. Sooner or later such methods should be applied to the Euphorbiaceae in general, and ideally to the Euphorbieae in particular, where there are inconsistencies in current generic delimitation. How, for instance, would a cladistic analysis relate *Chamaesyce*, very widely recognized as a distinct genus, to the various sections within *Euphorbia* subg. *Agaloma* and the rest of *Euphorbia*? There are many other interesting problems waiting to be tackled: What is the relationship between the Old World and New World species of *Euphorbia*? How do the subgenera *Euphorbia* and *Lacanthis* (sensu Gilbert, 1987) relate to the rest of the genus? Such an analysis, in my view, could do much to clarify these relationships and thus the taxonomy of the tribe as a whole. It would demand a much greater knowledge of the possible origins of the Euphorbieae than is available. In a group so morphologically isolated, speculation is needed.

The Euphorbieae and Hippomaneae are included within the subfamily Euphorbioideae along with three other tribes (Stomatocalyceae, Pachystromateae, and Hureae) that have usually been associated with the Hippomaneae (Webster, 1994), primarily on the basis of their caustic milky latex from nonarticulate laticifers, frequently glandular bracts, and often highly reduced flowers that always lack petals. This juxtapositioning has not always been the case: Mueller Argoviensis (1866) and Bentham (1878) placed these groups at opposite ends in their sequences. There are indeed major differences in inflorescence morphology between the two groups such that I felt forced to consider the possibility that the similarities were the product of convergence. One unusual cryptic character, very characteristic, rod-shaped starch grains found in the latex, is a good contender for a synapomorphy, which suggests that they do have a common origin. This in turn led to an attempt to reconstruct a possible ancestral inflorescence type from which the modern plants could have evolved most parsimoniously.

The rod-shaped starch grains have not been reported in other members of the Euphorbiaceae, although many taxa appear never to have been

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surveyed (Rudall, 1987), and their discovery elsewhere in the family would be a serious challenge to the taxonomic integrity of the Euphorbioideae. The toxicity of the latex has also been mentioned as a linking character but the major compounds involved—diterpene esters—occur also in subfamily Crotonoideae (Beutler et al., 1989). The pollen of the Euphorbioideae is rather uniform (Punt, 1987), but the pollen type is apparently plesiomorphic; thus the similarity should be treated with caution. Morphological evidence is even less clear-cut. There are superficial similarities in that most taxa in both groups have a sparse to nonexistent indumentum of simple hairs but there are many exceptions in both major tribes, such as species of *Chamaesyce* and *Agaloma* within *Euphorbia* and members of the Mabeinae and many species of *Stillingia* within the Hippomaneae, and such evidence can only be regarded as essentially negative: it does not disprove the possibility of a relationship. The tendency toward very reduced flowers, rare in the family as a whole, has also been invoked to support a common grouping. It is possible, theoretically, to select a reduction series for the flowers within the Hippomaneae from genera such as *Mabea*, which have well-defined perianths and male flowers with many stamens, through to *Dalembertia*, in which the male flower is reduced to a single sepal and a single stamen and the female flower has only vestigial remnants of the perianth. This sequence could be regarded as continued by the Euphorbieae, where the male flower is always reduced to a single naked anther and the female flower to a naked ovary. There is evidence of a female perianth in many genera within the Euphorbieae, including some species of *Euphorbia*, but the only clear indication of a male perianth, beyond an articulation between pedicel and filament, is the vestigial male perianth seen in *Anthostema* and *Dichostemma*. There has been a temptation to suggest that this sequence gives a true guide to relationships, but this must be questioned—could the Hippomaneae really have given rise directly to the Euphorbieae?

The major difference between the two groups is the inflorescence structure, which is discussed at length below. Details of floral morphology, most notably the very different styles, also suggest that the Euphorbieae and Hippomaneae may not be closely related. In the Euphorbieae the styles are relatively short, usually divided, and have more or less capitate stigmas. Studies indicate that most species are pollinated by a variety of often unspecialized insects, the exception being a group of New World taxa, most obviously the genus *Pedilanthus* but also various red-flowered *Euphorbia* species, pollinated by birds. In most members of the Hippomaneae the styles are undivided, long and tapered, and are usually characteristically circinately coiled when young. There are not many observations of pollination. The pendent inflorescences and long stigmas of some species suggest that wind pollination is a possibility, but other genera have well-developed nectaries within the inflorescences indicating some form of animal pollination, perhaps most often by small unspecialized insects (Bawa et al., 1985), but in at least one case, *Mabea occidentalis* Benth. (Steiner, 1983), predominantly by bats. Thus the significance of the striking differences in the styles is not clear. Another possibly significant difference is the frequency of succulence within the Euphorbieae where it has clearly evolved several times independently, whereas succulence appears to be almost absent in the Hippomaneae, recorded only from a few Brazilian species of *Stillingia* (Rogers, 1951).

The contrast in inflorescence organization between the Hippomaneae and the Euphorbieae seems so great that one must consider whether the similarities between them could be the result of convergence rather than an indication of common ancestry. If the most reasonable (parsimonious) hypothetical common ancestor has to have characters such that it would have to be placed within one of the other subfamilies, notably the Crotonoideae, rather than the Euphorbioideae, the Euphorbioideae would have to be regarded as a grade rather than a clade.

There seems to be little or no case for questioning the homogeneity of the tribe Euphorbieae as it is clearly defined by the very peculiar inflorescence—the cyathium—distinct from all other inflorescence types seen within the family. Linnaeus and other very early authors, plus one of the two giants of nineteenth-century Euphorbiaceae taxonomy, Baillon (1874), thought that the cyathium was a hermaphroditic flower. However, the alternative theory that it was an inflorescence was mentioned by Lamarck as early as 1788 and is now unquestioned, though there is still disagreement in the exact interpretation of its organization. The cyathium consists of a cupular receptacle with marginal lobes usually regularly alternating with glands, sometimes quite complex in structure, enclosing a whorl of groups of male flowers inserted below each lobe, plus their associated bracteoles, and a single, central female flower, often reduced to a naked ovary. There is quite a lot of variation within this theme with regard to features such as the number of parts within the involucre and the

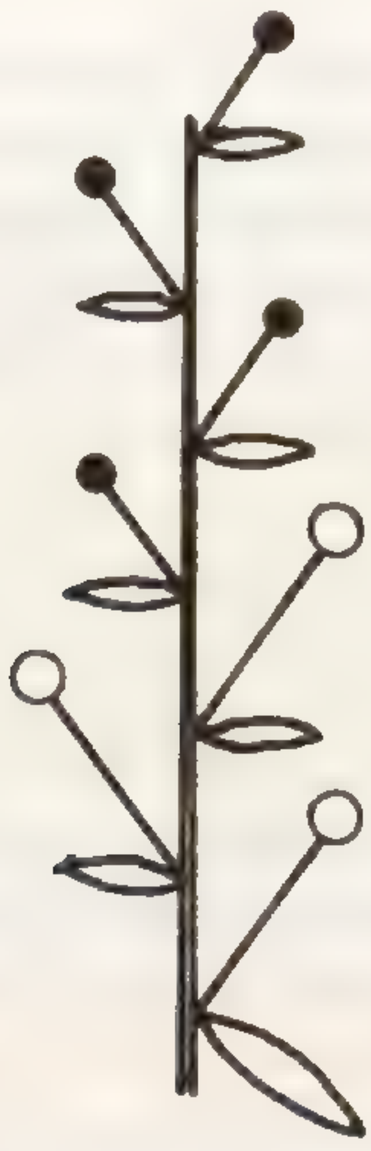
amount of fusion between them and the occasional presence of a small perianth on the male and female flowers, but no genera can be regarded as having inflorescences truly intermediate between a cyathium and any other inflorescence recorded within the family. There has been much debate on the nature of the cyathium but the weight of evidence (e.g., Schoute, 1937) seems to support the scheme suggested by Eichler (1878), in which each involucral lobe/bract subtends a monochasium of male flowers.

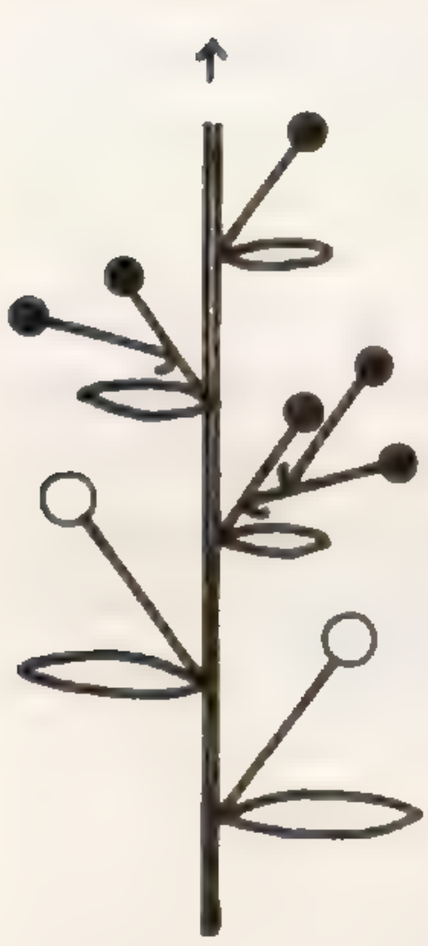
The cyathium contrasts very strongly in organization with the inflorescences of the vast majority of other members of the family, including the other tribes placed within subfamily Euphorbioideae by Webster. There is a fundamental division within the Euphorbiaceae between the uniovulate tribes, with only one ovule per ovary locule, and the biovulate tribes, with two ovules per locule. The biovulate tribes are distinct in so many features of anatomy and morphology that they will not be considered in detail. It might, however, be worth making the observation that the axillary fascicles of flowers characteristic of the vast majority of biovulate taxa must be considered rather specialized reduced inflorescences. Most other uniovulate tribes, including the Hippomaneae, have inflorescences that are generally regarded as cymose, but many show an essentially racemelike organization in which the cymose nature of the ultimate elements is only betrayed by the fact that some of the male flowers are in very reduced cymules rather than solitary as in a true raceme. The contrast with the Euphorbieae is further increased by the fact that, as in the vast majority of the genera of the Euphorbiaceae, the female flowers are proximal and the male flowers distal. Such an arrangement within an elongated inflorescence has a structural logic: female flowers produce bulky, longer-lived fruits requiring the transport of nutrients; male flowers are usually smaller, short-lived, and only require a transient supply of nutrients. It would be functionally illogical to have to maintain an extra length of stem at the base of an inflorescence once the male flowers had finished, especially as the extra length would mean that the stem would have to be that much stronger mechanically. By having distal male flowers, that part of the stem does not need to transport as many nutrients for so long, does not need to be strong enough to support relatively heavy fruits, and can be shut down as soon as the male flowers have dispersed their pollen. Having said this, there is an obvious exception to such logic—*Acalypha*—which shows a bewildering array of inflorescence types, particularly with regard to the relative positions of male and female flowers, and must be regarded as a special case.

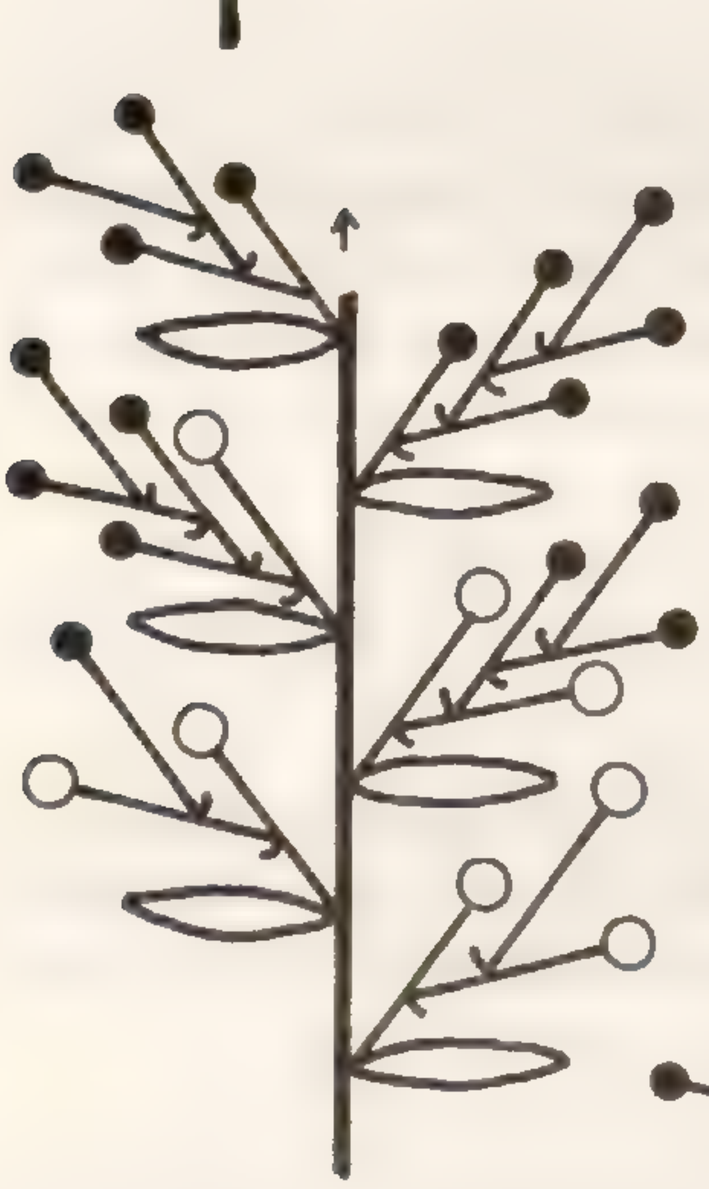
To convert a typical Hippomaneae inflorescence into a cyathium one must postulate a considerable condensation of the main inflorescence axis, a relatively straightforward and common evolutionary process. However, at the same time one must also postulate a complete reversal in the relative position of the male and female flowers or the loss of the proximal female flowers plus the de novo production of a terminal female flower. The latter process seems particularly difficult to account for unless one invokes the terminal allomorphic flowers seen in some species of *Acalypha*. There would also have to be a reversal of the general trend of the reduction of the distal male inflorescences. An alternative scheme would be to derive the cyathium from a group of thyrses. Such a scenario is very similar to that proposed below and must be given consideration. The one fact against it is the cymose arrangement of the groups of male flowers within the cyathium. It is difficult to imagine a racemelike inflorescence giving rise to such a grouping.

A more parsimonious scenario is to postulate that both the Hippomaneae and the Euphorbieae evolved from a common ancestor which had a thyrse—a synflorescence in which an indefinite fertile axis produced a spiral series of axillary bisexual cymes (Fig. 1). The cymes could be either dichasial or monochasial or, perhaps quite likely, initially dichasial with monochasial ultimate branches such as is frequently seen with *Jatropha*. The Hippomaneae inflorescence could (and surely did) evolve by a simple process of reduction with the proximal cymes being reduced to single female flowers and the distal cymes reduced to cymules of male flowers or eventually to single male flowers. The Euphorbieae would have to be derived by a more complex evolutionary process centered primarily on a great condensation of the main synflorescence axis to produce a dense head of cymes, the central one, perhaps in response to the protected situation, becoming reduced to a single female flower while the surrounding whorl of cymes became all male and their associated subtending bracts and ?stipular glands fused to form an involucre.

An alternative scenario is that the cyathium has evolved from a single cyme with a primary female flower and lateral male flowers such as is seen in *Jatropha*. Croizat (1938), in discussing *Veoguillauminea*, accepted such a scenario and expressed the belief that 4-lobed involucres were the basic type for the Euphorbieae, derived presumably from the initial two levels of branching of a dichasium.







An immediate difficulty is the frequency of 5-lobed involucres, which would be difficult to derive from a regular dichasial cyme but which could be expected as the norm if the involucre was the product of the condensation of a Fibonacci spiral derived from a thyrse. Two further bits of evidence argue against a development from a single cyme. First is the situation in *Neoguillauminea*, where the central female flower appears to be subtended by four separate involucres of male flowers, which indicates that several inflorescences are involved. Second, some species in *Euphorbia* sect. *Esula* (notably *E. cyparissioides* Pax) have groups of male flowers and glands very similar to those of the involucre intermingled within the involucre proper in a possible spiral series. Such a situation could be explained easily if the axis of the cyathium was a contracted synflorescence, but is very much more difficult to explain if the structure was derived from a single cyme.

Unmodified simple cymes are of rather rare occurrence within the family and among African taxa are only found in *Jatropha*, a genus showing a number of other apparently primitive features, most notably the well-developed corolla and female flowers with staminodes occasionally so well developed (e.g., in *J. tropaeolifolia* Pax) that the flowers appear to be bisexual. Another unusual character of *Jatropha* is the diversity of laticifer types, a feature that has been interpreted as an indication of primitiveness (Dehgan & Craig, 1978; Rudall, 1987). The cymes of most species of *Jatropha* are primarily dichasial, but in many species (*J. spicata* Pax is a good example) the ultimate branches are usually long monochasia of male flowers. This suggests that there is a natural tendency within the organization of such cymes for reduced terminal elements to be monochasial, which would support Eichler's (1878) interpretation of the cyathium.

Dehgan & Craig (1978) discussed the possibility of a *Jatropha*-like plant being ancestral to the Crotonoideae. It seems a distinct possibility that any common ancestor of the Hippomaneae and the Euphorbieae might also have had *Jatropha*-like cymes, thus opening up the question of subfamily relationships. The cymes of most *Jatropha* species are strictly terminal and show no tendency toward the production of a synflorescence. Perhaps the strictly terminal position of the inflorescence in such *Jatropha* is a factor in their having retained their clearly cymose organization while other groups with axillary cymes have evolved the thyrse (and cyathia?) now so widespread in the family. However, the most primitive species (Dehgan & Schutzman, 1994, this issue), *J. curcas* L., does produce a synflorescence such as is postulated here as the common ancestral form for cyathia and for the thyrses of most other uniovulate Euphorbiaceae. This would seem to reinforce the view that *Jatropha* might represent the nearest approach to an ancestral type for the family as a whole.

In conclusion, it is suggested that it is not possible for the cyathium to have evolved from any inflorescence found within modern-day Hippomaneae (and closely allied tribes). One must conjecture a rather primitive common ancestor belonging to neither group but rather to the Crotonoideae. If this is indeed the case, it might be better to extend the Euphorbioideae to include the Crotonoideae, as suggested in effect by Mahlberg et al. (1987). Alternatively, if an independent relationship of each group to a very primitive member of the family be accepted, there might be a good case for placing the Hippomaneae and allies in a subfamily of their own and restricting the Euphorbioideae to the Euphorbieae.

Literature Cited

Baillon, H. 1874. Euphorbiacées. *In:* Hist. Pl. 2: 105–256. Hachette, Paris.

Bawa, K. S., S. H. Bullock, D. R. Perry, R. E. Coville & M. H. Grayum. 1985. Reproductive biology of lowland rainforest trees II. Pollination systems. Amer. J. Bot. 72: 346–356.

Bentham, G. 1878. Notes on Euphorbiaceae. J. Linn. Soc., Bot. 17: 185–267 (pp. 201–204, 239–245).

Beutler, J. A., A. B. Alvarado, T. G. McCloud & G. M. Cragg. 1989. Distribution of phorbol ester bioactivity in the Euphorbiaceae. Phytotherapy Research 3: 188–192.

Croizat, L. 1938. Notes on the Euphorbiaceae, with a new genus of the Euphorbieae. Philipp. J. Sci. 64: 397–412.

Dehgan, B. & M. E. Craig. 1978. Types of lacticifers and crystals in *Jatropha* and their taxonomic implications. Amer. J. Bot. 65: 345–352.

Figure 1. Diagrammatic representation of the hypothetical evolution of, on the left, the racemelike inflorescences of the Hippomaneae (and most other Crotonoideae and Acalyphoideae) and, on the right, the cyathium from a hypothetical synflorescence of axillary bisexual cymes. For simplicity the cymes are shown as monochasia, but in practice are more likely to be primarily dichasial. On the left there is a progressive elongation of the main axis and reduction of the axillary cymes. On the right there is a shortening of the main axis to form a dense cluster of cymes, a central, terminal cyme becoming reduced to a single female flower and surrounded by a whorl of all-male cymes, while the associated subtending leaves and stipules fuse to form an enclosing involucre.

——— & B. SCHUTZMAN. 1994. Contributions toward a monograph of neotropical *Jatropha*: Phenetic and phylogenetic analyses. Ann. Missouri Bot. Gard. 81: 349–367.

EICHLER, A. W. 1878. Blüthendiagramme construit und erläutert, 2. W. Engelmann, Leipzig.

GILBERT, M. G. 1987. Two new geophytic species of *Euphorbia* with comments on the subgeneric groupings of the African members of the genus. Kew Bull. 42: 231–244.

LAMARCK, J. B. A. P. M. DE. 1788. Euphorbe ou Tithymale, *Euphorbia*; Caractère Générique. Encycl. 5: 413.

MAHLBERG, P. G., D. G. DAVIS, D. S. GALITZ & G. D. MANNERS. 1987. Lacticifers and the classification of *Euphorbia*: The chemotaxonomy of *Euphorbia esula* L. Bot. J. Linn. Soc. 94: 165–180.

MUELLER ARGOVIENSIS, J. 1866. Euphorbiaceae. *In:* A. P. de Candolle, Prodr. 15(2): 1–1286.

PUNT, W. 1987. A survey of pollen morphology in Euphorbiaceae with special reference to *Phyllanthus*. Bot. J. Linn. Soc. 94: 127–142.

ROGERS, D. J. 1951. A revision of *Stillingia* in the New World. Ann. Missouri Bot. Gard. 38: 207–259.

RUDALL, P. J. 1987. Lacticifers in Euphorbiaceae—A conspectus. Bot. J. Linn. Soc. 94: 14–163.

SCHOUTE, J. C. 1937. On the aestivation in the cyatheum of *Euphorbia fulgens*, with some remarks on the morphological interpretation of the cyathium in general. Recueil Trav. Bot. Néerl. 34: 168–181.

STEINER, K. E. 1983. Pollination of *Mabea occidentalis* (Euphorbiaceae) in Panama. Syst. Bot. 8: 105–117.

WEBSTER, G. L. 1994. Synopsis of the genera and suprageneric taxa of Euphorbiaceae. Ann. Missouri Bot. Gard. 81: 33–144.

PATTERNS OF DIVERSIFICATION AND EVOLUTION IN *PHYLLANTHUS ODONTADENIUS* (EUPHORBIACEAE)[1]

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Abstract

Experimental crossings within *Phyllanthus* subsect. *Odontadenii* reveal different levels of reproductive incompatibility between taxa of varying morphological distinction. Some of the reproductive barriers may be circumvented using in vitro culture. Cytological and morphological studies of the progeny of experimental crosses has yielded information about the processes of differentiation of taxa within subsection *Odontadenii*, as well as within the *Phyllanthus urinaria* complex. The results of this study support the recognition of taxa earlier proposed in these two complexes, and furthermore document the existence of a tetraploid taxon (*Phyllanthus magnificens*) with a base chromosome number of $x = 10$.

This work is part of a long-range research program carried out at the Laboratoire de Morphogénèse at Orsay. Our goal has been to utilize taxa of *Phyllanthus*, a genus lending itself to experimental analysis, in order to understand the genetic processes involved in differentiation of populations and species.

In presenting the findings of this study, we will try to provide a synthesis of our results with the previous experimental studies on herbaceous species of *Phyllanthus*, including those on *Phyllanthus* subsect. *Odontadenii* (Tran Ha & Bancilhon-Rossignol, 1976; Tran Ha et al., 1976; Belliard & Besse, 1980; Brunel & Roux, 1981) and on the *Phyllanthus urinaria* complex (Haïcour, 1983, 1984a, b; Rossignol et al., 1987).

Two complexes of closely related species that differ in geographic distribution, basic chromosome numbers, morphological characteristics, and polymorphism were studied for this article. (1) *Phyllanthus odontadenius* subsect. *Odontadenii* originated from Africa. This study considers it as a complex containing eight species with three basic chromosome numbers ($x = 6$, $x = 7$, $x = 9$) but very homogeneous morphological characteristics (Brunel & Roux, 1981): *P. braunii* (Pax) Hutch. ($2n = 12$), *P. mieschii* Brunel & Roux ($2n = 18$), *P. odontadenius* Muell. Arg. ($2n = 24$), *P. gagnioevae* Brunel & Roux ($2n = 28$), *P. magnificens* Brunel & Roux ($2n = 36$), *P. bancilhonae* Brunel & Roux ($2n = 56$), *P. jaegeri* Brunel & Roux, and *P. mannianus* Muell. (with unknown karyotypes). *Phyllanthus braunii* has three morphotypes: *P. braunii* (12b, the typical form), *P. braunii* (12l, with long branchlets), and *P. braunii* (12m, with brown leaves). *Phyllanthus braunii* (typical form) and its two variants were each crossed with *P. odontadenius*, *P. gagnioevae*, *P. bancilhonae*, and *P. magnificens*. (2) The *Phyllanthus urinaria* complex originated from eastern Asia. It contains various morphotypes but only one basic chromosome number has currently been described ($x = 25$). Recently two groups, spiraled (S) and radiated (R), have been distinguished within the *P. urinaria* complex using seed ornamentation (Haïcour, 1983; Rossignol et al., 1987). Each group contains diploid ($2n = 50$) and tetraploid taxa ($2n = 100$).

Our studies are focused on three areas: (1) the sexual incompatibility phenomena seen in experimental crossings of taxa from West Africa characterized by different chromosome numbers. (2) A cytological study of hybrids obtained from different crossings, either in greenhouse conditions or after culturing extracted embryos in vitro (differences

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in fertility of hybrids are noted). Finally, we include (3) a preliminary morphological study of the various parental groups and of some of the hybrids obtained.

Materials and Methods

PLANT MATERIAL

Plant material used in this study came from taxa of *Phyllanthus* maintained in greenhouses of the Institute of Plant Biology, Faculté des Sciences at Orsay. It includes five groups, easily identified by morphology and karyotype, which Brunel & Roux (1981) delimited as species of subsection *Odontadenii* in section *Phyllanthus*. The taxa included are:

Phyllanthus braunii (Pax) Hutch. $2n = 12$. Three morphotypes were found in a single population near Abidjan, Côte d'Ivoire: the typical form (12b) and the two variant forms (12l with long branchlets, 12m with brown leaves).

Phyllanthus odontadenius Muell. Arg. $2n = 24$, from Bouaflé, Côte d'Ivoire. Our material appeared closest to the typical element of Mueller's species.

Phyllanthus gagnioevae Brunel & Roux $2n = 28$, from a population of seeds collected near Bouaké, Côte d'Ivoire; most of the seeds from this locality were very close to the next species.

Phyllanthus bancilhonae Brunel & Roux $2n = 56$, from Bouaké.

Phyllanthus magnificens Brunel & Roux, collected by Brunel in Togo and described as a taxon with $2n = 36$ (Brunel & Roux, 1981); the present study describes it as a taxon with $2n = 40$.

We consider that *Phyllanthus odontadenius* may be regarded as the tetraploid form of the diploid species *P. braunii*, with a basic chromosome number of 6. *Phyllanthus bancilhonae*, in like manner, may be regarded as the octoploid form of the tetraploid *P. gagnioevae*, with a basic number of 7. It should be noted that *P. bancilhonae* and *P. gagnioevae* were grown from the same population of seeds.

Except for *P. magnificens*, the species mentioned above had already been experimentally crossed (Tran Ha & Bancilhon-Rossignol, 1976; Tran Ha et al., 1976; Belliard & Besse, 1980). We extended this work by testing the degree of interspecific compatibility in crosses between these species and *P. magnificens*. Different populations of *P. braunii* (3 from Côte d'Ivoire, 2 from Cameroon), *P. odontadenius* (1 from Côte d'Ivoire, 4 from Cameroon, 1 from Togo), and *P. gagnioevae* (1 from Côte d'Ivoire, 1 from Togo) were used.

All these species of *Phyllanthus* are herbaceous, with stems more or less ligneous at the base, and pluriannual (annual but sometimes living into one or more additional years). The plagiotropic branchlets with lateral ribs (characteristic of subsect. *Odontadenii*) always have staminate inflorescences at the proximal nodes, with usually solitary pistillate flowers at the distal nodes. The staminate flowers have six sepals and three stamens with filaments connate but anthers free; pistillate flowers have six sepals, a variable disk, and smooth ovary; seeds are dorsally ornamented with longitudinal ribs.

METHODS

Crossing and fertility testing of hybrids

The crossing and fertility testing of hybrids could be made in our greenhouses only during the warm season, from late spring to autumn. Plants were cloned using cuttings, each month-old cutting beheaded in order to encourage growth of orthotropic axes, and crossing experiments were conducted six weeks later.

For each crossing program, four clonal plants were emasculated (by removing staminate flowers and buds), and axillary orthotropic buds (bos, Fig. 1) were cut off to eliminate any possibility of staminate flower production. A week after the first emasculation, all pistillate flowers that appeared to have been fertilized were removed, and pollen grains from the appropriate staminate donor were manually deposited on the receptive stigmas. After marking leaves corresponding to flowers, the operation was repeated three days consecutively (on newly receptive pistillate flowers).

Using the same protocol, a single plant was self-fertilized as the control. All the plants treated were isolated with transparent paper bags in order to avoid alien pollen.

Seeds produced by hybrid plants were then transferred to soil with peat as soon as the first green leaves appeared.

For fertility tests, we carried out self-fertilizations and backcrosses with parental plants.

In vitro embryo culture

In some crosses that produced plants with fruits dropping before complete ripeness, we harvested the fruits 13 days after pollination and sterilized them. The immature seeds were transferred in the dark to a medium with high osmotic pressure [Monnier salts (Monnier, 1973) + saccharose 120 g liter + glucose 200 g/liter + glutamine 400 g liter] in a sterile Petri dish. About 30 to 40 days later, when the juvenile plant had grown sufficiently to burst the testa of the seed, we made a second

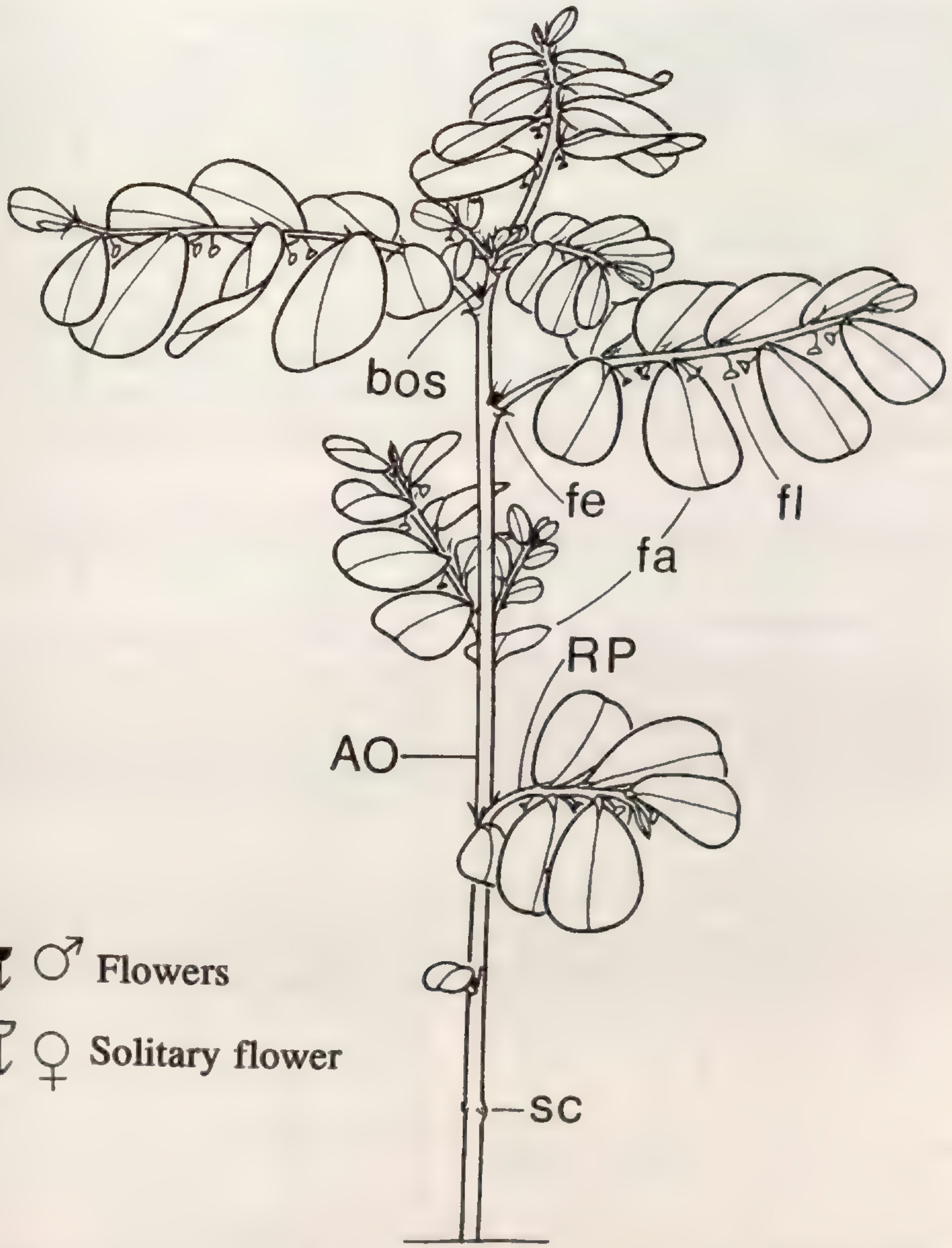


FIGURE 1. Architectural scheme of a *Phyllanthus* from the *P. odontadenius* complex. Original characteristic: 4 green leaves above the cotyledons. sc = scars of cotyledons; AO = orthotropic axis; RP = deciduous branchlet; fa = green leaf; fe = cataphyll; bos = secondary orthotropic bud; fl = solitary pistillate flower.

transfer in daylight onto a medium containing only saccharose (20 g/liter), without any amino acid. Young plants can be obtained in a short time and then grown out on soil compost.

Cytological observation

The techniques used in this study have been previously described by Tran Ha & Bancilhon-Rossignol (1976).

Mitotic cells were studied using young root apices. Roots were immersed in α-chloronaphthalene, fixed in acetic alcohol (¾ - ¼), washed, hydrolized in chlorhydric acid, colored with Schiff reagent, and squashed between two glass cover slips in a Merck aceto-carmine solution.

For meiotic observations, staminate floral buds were fixed in 5% Carnoy solution, dissected to separate the pollen mother cells, and squashed in Merck aceto-carmine solution.

Pollen grains were obtained for morphological observation by squashing mature anthers in 2% Merck aceto-carmine solution.

CULTURE CONDITIONS

Plant culture conditions in the tropical greenhouses at Orsay were as follows: humidity 70–80%, temperature 25–40°C, daylight with complementary artificial light. Plants were vegetatively propagated on a stable soil compost.

RESULTS

CROSSINGS

Crossings in greenhouse conditions

Two series of experimental crossings were made. First, 36 crosses were made between the six taxa from Côte d'Ivoire: three morphs of *P. braunii* ($2n = 12$), and single forms of *P. odontadenius* ($2n = 24$), *P. gagnioevae* ($2n = 28$), and *P. bancilhonae* ($2n = 56$). A second series of crosses was made between these taxa and *P. magnificens* ($2n = 40$). The results were the same when using different plants of the same population.

The results of the total of 49 crossings accomplished are given in Table 1. The crossings included seven auto-fertilizations (pistillate flowers from one taxon pollinated with pollen from the same taxon), and 42 cross-pollinations. All experimental pollinations resulted in seed set, the ovaries becoming inflated 4 or 5 days after pollination. When physical conditions of flowers were optimal, nearly 100% of "nouaisons" (swelling of ovary) could be obtained from self-pollinations.

Among the 42 cross-pollinations, the only ones giving almost the same result as self-pollination (I_1) are the crosses between the 12l and 12m forms of *P. braunii*. In all other crossings between two different taxa, the success rate depends on the genotypes concerned and the directionality of the cross. The success rate, in any event, is always smaller than self-fertilization (I_1). Only 20 of the 42 cross-pollinations yielded viable F_1 hybrids.

In 22 crossings out of 42, there was no viable progeny. Fruits aborted, even though well developed, 10 to 18 days after pollination (see Table 1). Such fruits are characterized by abnormal seeds with either flabby teguments and rudimentary embryo, or well-developed teguments with unviable embryo.

The degree of delay in fruit abortion does not appear well correlated with the state of development of the seeds. On the other hand, there appears to be a relation between the seed condition and directionality of the cross. For example, in crossing between *P. braunii* ($2n = 12$) and *P. bancilhonae* ($2n = 56$), or between *P. braunii* and *P. odontadenius* ($2n = 24$), we never observed the presence of an embryo (SE) when the staminate parent is one of the three taxa with $2n = 12$, whereas there is always an embryo developed when any of the $2n = 12$ taxa are used as the pistillate parent. Similar results were found in the crossings of *P. braunii* (forms 12l and 12m) with *P. gagnioevae*, where the embryo is viable or not depending on the directionality of the cross.

Several features of the crossing program stand out. First, no compatible crosses were obtained between taxa with the same base chromosome number but different ploidy, e.g., between diploid and tetraploid (*P. braunii* × *P. odontadenius*) or between tetraploid and octoploid (*P. gagnioevae* × *P. bancilhonae*).

In contrast, a strong genetic relationship exists among the taxa of *P. braunii*, especially between 12l and 12m; the results of a cross between those two forms are very similar to those of a self-fertilization. Nevertheless, a slight incompatibility barrier ("mother effect") may be detected between 12b in relation to 12l and 12m.

Incompatibility barriers have also been demonstrated between *P. braunii* ($2n = 12$) and the taxa *P. bancilhonae* ($2n = 56$), *P. gagnioevae* ($2n = 28$), and *P. magnificens* ($2n = 40$); between *P. bancilhonae* ($2n = 56$) and *P. magnificens* ($2n = 40$) or *P. odontadenius* ($2n = 24$); between *P. gagnioevae* ($2n = 28$) and *P. magnificens* ($2n = 40$) or *P. odontadenius* ($2n = 24$); and between *P. magnificens* ($2n = 40$) and *P. odontadenius* ($2n = 24$) (Table 2).

In vitro embryo culture in case of non-viable progeny

In crossings yielding no viable progeny, we have observed a kind of embryo rejection prior to maturation of the seed. The isolation of the seed at a precocious stage (about 13 days after fertilization) and its culture on an appropriate medium has permitted seedling development. Rapid transformation of the seedling into a mature hybrid plant was achieved by changing the culture medium, removing plantlets to vermiculite, and planting in the ground. This technique was perfected in obtaining seeds from the pistillate $2n = 56$ × staminate $2n = 28$ crossing, and them repeated for other crossings (Table 2). Hybrid plants were obtained in all instances.

TABLE 1. Results from crossings between various genetic entities of *Phyllanthus odontadenius* in greenhouse conditions. First generation I_1 and F_1 descendants from auto- or heterocrossings. *T = fruit abortion (diagonally striped boxes); SE = seed without embryo; Ep = seed with minute embryo; Ed = seed with dessicated embryo; M = meiosis (MN, normal meiosis; MA, aberrant meiosis; MTA, very aberrant meiosis).*

♀ \ ♂	*P. bancilhonae*	*P. magnificens*	*P. gagnioevae*	*P. odontadenius*	*P. braunii* typical	*P. braunii* long branchlets	*P. braunii* brown leaves
	56 chr.	40 chr.	28 chr.	24 chr.	12b	12 chr. 12l	12m
P. bancilhonae 56	I_1	F_1 close to 56 48 chr. sterile MTA	T (circ. 13 - 14d) Ep	F_1 40 chr. sterile MTA	T(circ. 10 - 11d) SE	T(circ. 10d) SE	T(circ. 10d) SE
P. magnificens 40	F_1 close to 56 48 chr. sterile MTA	I_1	F_1 34 - 32 chr. sterile MTA	F_1 32 chr. sterile MTA	T(circ. 16d) SE	T(circ. 16d) SE	T(circ. 16d) SE
P. gagnioevae 28	T(circ. 15 - 16d) Ed	F_1 34 - 32 chr. sterile MTA	I_1	F_1 26 chr. sterile MTA	F_1 20 - 24 - 26 sterile MTA	F_1 20 - 24 - 26 chr. sterile MTA	F_1 20 chr. sterile MTA
P. odontadenius 24	F_1 40 chr. sterile MTA	F_1 32 chr. sterile MTA	F_1 26 chr. sterile MTA	I_1	T(circ. 11d) SE	T(circ. 14d) SE	T(circ. 15d) SE
P. braunii 12b	T(circ. 10 - 12d) Ep	T(circ. 10 - 15d) SE	F_1 20 - 24 - 26 chr. sterile MTA	T(circ. 16d) Ed	I_1	F_1 12 chr. MA	F_1 12 chr. MA
P. braunii 12l	T(circ. 12 - 14d) Ep	T(circ. 10 - 15d) SE	T(circ. 15 - 18d) Ed	T(circ. 12 - 14d) Ed	F_1 12 chr. MA	I_1	F_1 12 chr. MN
P. braunii 12m	T(circ. 14d) Ep	T(circ. 10 - 15d) SE	T(circ. 15 - 18d) Ed	T(circ. 15d) Ed	F_1 12 chr. MA	F_1 12 chr. MN	I_1

TABLE 2. Karyotypic results from crossings; progeny present or not depending on cross. SE = seed without embryo; Ed = seed with desiccated embryo.

Crossings	Results in greenhouse	After in vitro culture
Fruit abortion and no progeny except after in vitro culture (22 cases)		
♀ *P. bancilhonae* × ♂ *P. gagnioevae* (56 = 8 × 7) (28 = 4 × 7)	No descent (Ep)	F_1 42 chr.
♀ *P. gagnioevae* × ♂ *P. bancilhonae*	No descent (Ed)	F_1 42 chr.
♀ *P. bancilhonae* × ♂ *P. braunii* typical (12b) (56 = 8 × 7) (12 = 2 × 6)	No descent (SE)	
♀ *P. braunii* typical (12b) × ♂ *P. bancilhonae*	No descent (Ep)	F_1 34 chr.?
♀ *P. bancilhonae* × ♂ *P.* long branchlets (12l) (56 = 8 × 7) (12 = 2 × 6)	No descent (SE)	
♀ *P.* long branchlets (12l) × ♂ *P. bancilhonae*	No descent (Ep)	F_1 34 chr.?
♀ *P. bancilhonae* × ♂ *P.* brown leaves (12m) (56 = 8 × 7) (12 = 2 × 6)	No descent (SE)	
♀ *P.* brown leaves (12m) × ♂ *P. bancilhonae*	No descent (Ep)	F_1 34 chr?
♀ *P. magnificens* × ♂ *P. braunii* typical (12b) (40 = 4 × 10) (12 = 2 × 6)	No descent (SE)	
♀ *P. braunii* (12b) × ♂ *P. magnificens*	No descent (SE)	
♀ *P. magnificens* × ♂ *P.* long branchlets (12l) (40 = 4 × 10) (12 = 2 × 6)	No descent (SE)	
♀ *P.* long branchlets (12l) × ♂ *P. magnificens*	No descent (SE)	
♀ *P. magnificens* × ♂ *P.* brown leaves (12m) (40 = 4 × 10) (12 = 2 × 6)	No descent (SE)	
♀ *P.* brown leaves (12m) × ♂ *P. magnificens*	No descent (SE)	
♀ *P. odontadenius* × ♂ *P. braunii* typical (12b) (24 = 4 × 6) (12 = 2 × 6)	No descent (SE)	
♀ *P. braunii* typical (12b) × ♂ *P. odontadenius*	No descent (Ed)	F_1 18 chr.?
♀ *P. odontadenius* × ♂ *P.* long branchlets (12b) (24 = 4 × 6) (12 = 2 × 6)	No descent (SE)	
♀ *P.* long branchlets (12l) × ♂ *P. odontadenius*	No descent (Ed)	
♀ *P. odontadenius* × ♂ *P.* brown leaves (12m) (24 = 4 × 6) (12 = 2 × 6)	No descent (SE)	F_1 18 chr.?
♀ *P.* brown leaves (12m) × ♂ *P. odontadenius*	No descent (Ed)	F_1 18 chr.?
♀ *P.* long branchlets (12l) × ♂ *P. gagnioevae*	No descent (Ed)	unknown result
♀ *P.* brown leaves (12m) × ♂ *P. gagnioevae*	No descent (Ed)	unknown result
Sterile hybrid F_1 (14 cases)		
♀ *P. bancilhonae* × ♂ *P. magnificens* (56 = 8 × 7) (40 = 4 × 10)	F_1 48 chr.	
♀ *P. magnificens* × ♂ *P. bancilhonae*	F_1 48 chr.	
♀ *P. bancilhonae* × ♂ *P. odontadenius* (56 = 8 × 7) (24 = 4 × 6)	F_1 40 chr.	
♀ *P. odontadenius* × ♂ *P. bancilhonae*	F_1 40 chr.	
♀ *P. magnificens* × ♂ *P. gagnioevae* (40 = 4 × 10) (28 = 4 × 7)	F_1 34-32 chr.	
♀ *P. gagnioevae* × ♂ *P. magnificens*	F_1 34-32 chr.	
♀ *P. magnificens* × ♂ *P. odontadenius* (40 = 4 × 10) (24 = 4 × 6)	F_1 32 chr.	
♀ *P. odontadenius* × ♂ *P. magnificens*	F_1 32 chr.	
♀ *P. gagnioevae* × ♂ *P. odontadenius* (28 = 4 × 7) (24 = 4 × 6)	F_1 26 chr.	
♀ *P. odontadenius* × ♂ *P. gagnioevae*	F_1 26 chr.	
♀ *P. gagnioevae* × ♂ *P. braunii* typical (12b) (28 = 4 × 7) (12 = 2 × 6)	F_1 20-24-26 chr.	
♀ *P. braunii* typical (12b) × ♂ *P. gagnioevae*	F_1 20-24-26 chr.	

TABLE 2. Continued.

Crossings	Results in greenhouse	After in vitro culture
♀ *P. gagnioevae* × ♂ *P.* long branchlets (12l)	F_1 20-24-26 chr.	
♀ *P. gagnioevae* × ♂ *P.* brown leaves (12m)	F_1 20 chr.	
Partially fertile hybrid F_1 (4 cases)		
♀ *P. braunii* typical (12b) × ♂ *P.* brown leaves (12m)	F_1 12 chr.	
♀ *P.* brown leaves (12m) × ♂ *P. braunii* typical (12b)	F_1 12 chr.	
♀ *P. braunii* typical (12b) × ♂ *P.* long branchlets (12l)	F_1 12 chr.	
♀ *P.* long branchlets (12l) × ♂ *P. braunii* typical (12b)	F_1 12 chr.	
Totally fertile hybrid F_1 (2 cases)		
♀ *P.* long branchlets (12l) × ♂ *P.* brown leaves (12m)	F_1 12 chr.	
♀ *P.* brown leaves (12m) × ♂ *P.* long branchlets (12l)	F_1 12 chr.	

CYTOLOGICAL ANALYSIS OF PROGENY

Chromosome counts

It was first necessary to confirm the chromosome number in *P. magnificens*, which was reported by Brunel & Roux (1981) as a hexaploid with $x = 6$. This chromosome number appeared probable to Brunel and Roux because of the morphological similarities and similar geographic distributions shown by the related species *P. odontadenius* ($2n = 24$) and *P. braunii* ($2n = 12$).

However, in examining *P. magnificens*, we always found the chromosome number to be $2n = 40$. To confirm this, we sent samples to P. Kupfer (Neuchatel), who also found a count of 40 chromosomes. He also noticed the presence in *P. magnificens* of two satellite-bearing chromosomes in which the satellites are not identical (Fig. 2A, A′).

The results obtained for chromosome counts from F_1 hybrids are recorded in Tables 1 and 2. Numbers such as 48 (Fig. 2C, C′), 42, 40, 34, 32 (Fig. 2B, B′), 26, 20, and 12 represent exactly half of the chromosome count of the respective parents, and help to confirm the hybrid nature of the plants examined.

Studies of meiosis

Three categories of F_1 hybrids may be recognized.

(1) Meiosis always extremely abnormal (MTA in Table 1): little pairing, with numerous univalents in metaphase I and bridges in anaphase I. This occurred in 14 cases from the following crosses:

♀ 28 × ♂ 12l ♀ 28 × ♂ 12m ♀ 28 × ♂ 12b ♀ 12b × ♂ 28

♀ 56 × ♂ 24 ♀ 24 × ♂ 56 ♀ 40 × ♂ 24 ♀ 24 × ♂ 40

♀ 28 × ♂ 24 ♀ 24 × ♂ 28 ♀ 56 × ♂ 40 ♀ 40 × ♂ 56

♀ 40 × ♂ 28 ♀ 28 × ♂ 40

(2) Meiosis with some anomalies (MA in Table 1), especially an abnormal number of bivalents in metaphase I (i.e., 4 or 5 bivalents instead of 6).

♀ 12b × ♂ 12l ♀ 12l × ♂ 12b ♀ 12b × ♂ 12m ♀ 12m × ♂ 12b

(3) Meiosis perfectly normal, with all chromosomes paired (MN in Table 1).

♀ 12l × ♂ 12m ♀ 12m × ♂ 12l

PRELIMINARY MORPHOLOGICAL ANALYSIS OF HYBRIDS AND PARENTAL POPULATIONS

We found a striking homogeneity of F_1 hybrids from the same crossing. It is very difficult (without precise biometrical measurement) to distinguish between reciprocal hybrids of a given species cross, whereas these hybrids are very easily distinguished from any hybrids obtained from crossing between other species.

Hybrid nature can be visually determined (Table 3; Figs. 3, 4 for crossings 24 × 40 and 56 × 40) by intermediate morphology between the two parents; predominant characters from one parent (where chromosome number is different, e.g., in 56 × 40 hybrids are closer to 56 parent); or heterosis effect.

A biometric study on the six taxa from Côte d'Ivoire gave similar characters between plants with $2n = 12$ (12l and 12m) and $2n = 24$ on the one hand, and between $2n = 28$ and 56 on the other (Tran Ha & Bancilhon-Rossignol, 1976). On the basis of this, we concluded that *P. odontadeni-*

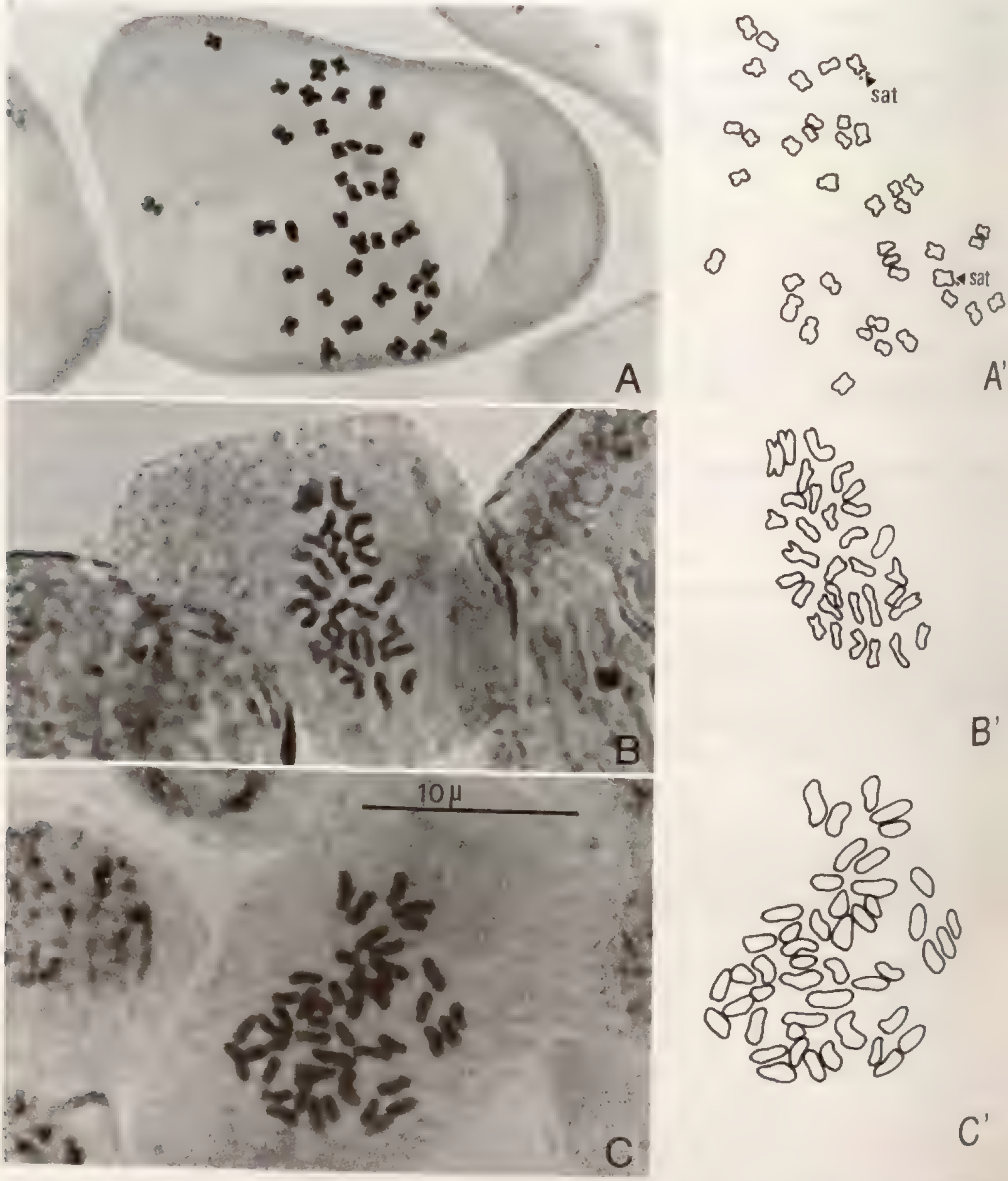


FIGURE 2. Photographs and line drawings of chromosome complements.—A, A'. *Phyllanthus magnificens*, $2n = 40$. A', line drawing showing 2 chromosomes with satellites (indicated by markers).—B, B'. Chromosomes of F hybrid (♀ *P. odontadenius* (24) × ♂ *P. magnificens* (40)).—C, C'. Chromosomes of F_1 hybrid (♀ *P. magnificens* (40) × ♂ *P. bancilhonae* (56)).

us represents the tetraploid form related to the diploid *P. braunii*, and *P. bancilhonae* the octoploid form related to *P. gagnioevae*.

EXAMINATION OF POLLEN FROM F_1 HYBRIDS—FERTILITY

The classification of F_1 hybrids from pollen grain examination agrees with the preceding one established from studies of meiosis. Thus we observed in hybrids with very abnormal meiosis (MTA) that the pollen is very heterogeneous, with grains differing in shape and length, and sometimes aberrant (heteropolar) or deformed.

In plants with abnormal meiosis (MA), there is less heterogeneity in the pollen, and in hybrids from crossing 12l with 12m, the pollen grains appear quite normal. That is not surprising, since anom-

TABLE 3. Morphological comparison between characters from parents and hybrids. Degree of pedicel length indicated by symbols +, ++, +++, ++++. L/l = length/width.

Parameters	Genotype		
	P. odontadenius $2n = 24$	*P. magnificens* $2n = 40$	Hybrids 24×40
Deciduous branchlet			
Number of green leaves	38 (16–50)	14 (6–20)	22 (15–21)
Leaf blade form	subquadrangular	ovoid with acute red apiculum	ovoid lightly acute
Number of secondary veins	5 pairs	5–6 pairs	6 pairs
L/l	1.4–1.6	1.7–2	1.7–2
♀ flower			
Flower and pedicel length	+	++	++
Calyx-lobe characteristics	acute and thin with white-edged vein	broad, rounded at the tip with red-edged vein	acute and thin with rosy-edged vein
Style characteristics	bifid style with green branches close together	bifid style with red branches apart	bifid style with rosy branches apart
Disk characteristics	continuous, crenulate	dissected into 6 segments	dissected into 6 segments

Parameters	Genotype		
	P. bancilhonae $2n = 56$	*P. magnificens* $2n = 40$	Hybrids 56×40
Deciduous branchlet			
Number of green leaves	36 (20–49)	16 (6–20)	28 (18–30)
Leaf blade form	broadly ovate	ovoid with acute red apiculum	broadly ovate
Number of secondary veins	4 pairs	5–6 pairs	7 pairs
L/l	1.8–2	1.6–1.8	1.8–2
Terminal ♀ flower	present	missing	present
♀ flower			
Flower and pedicel length	+++	++	++++
Calyx-lobe characteristics	broad and sharp, with green-edged vein	broad, rounded at the tip with red-edged vein	intermediate color and form
Style characteristics	sloping style with green branches	more raised style with red branches	style with intermediate slope and rosy branches
Disk characteristics	continuous, crenulated, edge slightly 6-lobed	dissected into 6 segments	dissected into 6 segments

alies in meiosis would be expected to induce abnormal tetrads and aberrant pollen grains.

Hybrids (F_1) from taxa with different chromosome numbers (Table 2) are sterile. After manual self-pollination, fruits are formed but they invariably abort within about 10 days. The seeds have flaccid teguments containing a liquid without an embryo or with an abnormally pale embryo.

Backcrossings of F_1 hybrids with parents give a negative result, as did crossing between two reciprocal hybrids. The F_1 generation is therefore completely sterile.

Among six hybrids obtained by crossing taxa with 12 chromosomes (*P. braunii*), the four hybrids from 12b × 12l and 12b × 12m are weakly fertile, while the hybrids from 12l × 12m are totally fertile (Table 3).

DISCUSSION AND CONCLUSIONS

The results of our studies appear to be of some interest, especially when they are compared with comparable studies of the *Phyllanthus urinaria* complex of eastern Asia (Haïcour, 1983).

In the *Phyllanthus odontadenius* complex (subsect. *Odontadenii*) we identified five taxa with a different karyotype, with diploid complements of 12, 24, 28, 40, and 56 chromosomes. One taxon, identified as *P. braunii*, includes three subgroups: 12b, 12l, and 12m (Fig. 5A).

FIGURE 3. Deciduous branchlets and pistillate flowers of *Phyllanthus bancilhonae* ($2n = 56$), *P. magnificens* ($2n = 40$), and the two hybrids.—A, A′. Deciduous branchlet and ♀ flower of parent 56.—B, B′. Deciduous branchlet and ♀ flower of hybrid 56 × 40.—C, C′. Deciduous branchlet and ♀ flower of hybrid 40 × 56.—D, D′, Deciduous branchlet and ♀ flower of parent 40.

In our earlier studies of the *Phyllanthus urinaria* complex, two ensembles based on seed ornamentation were distinguished: *Spiraled* (S) and *Radiated* (R), each of which includes cytotypes with 50 and 100 chromosomes. Four groups can therefore be recognized: 50S, 100S, 50R, 100R; the 50R group is polymorphic with two subgroups: 50R1 and 50R2 (Fig. 5B).

As a result of our crossing programs using taxa within the *Phyllanthus odontadenius* and *P. urinaria* complexes, it appears that there are reproductive barriers between taxa not previously recognized by earlier workers. In some instances, the barriers to intertaxon crossing are almost absolute, and indicate that considerable divergence has occurred.

Consequently, we consider *Phyllanthus odontadenius* and *P. urinaria* in the broad, traditional sense to represent complexes of closely related species. In the *P. urinaria* complex it is possible to make some inferences about the direction of evolution if we consider the 50S group to be most primitive (50S plates were found only in the supposed original country). The 50R group may then be considered as a mutant form with some novel characters; this group appears to be in an active stage of diversification and has extended beyond the original center (50R1).

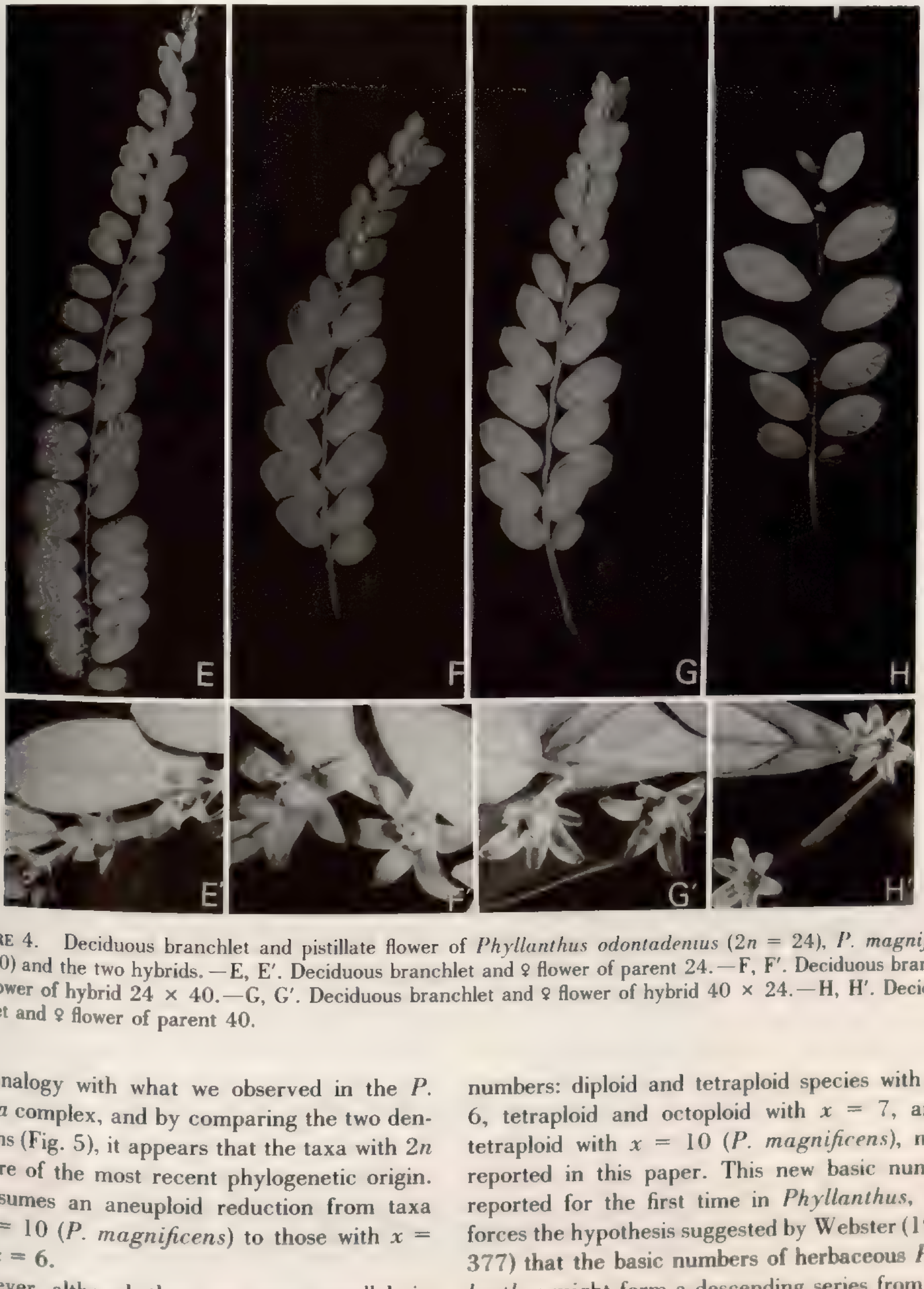


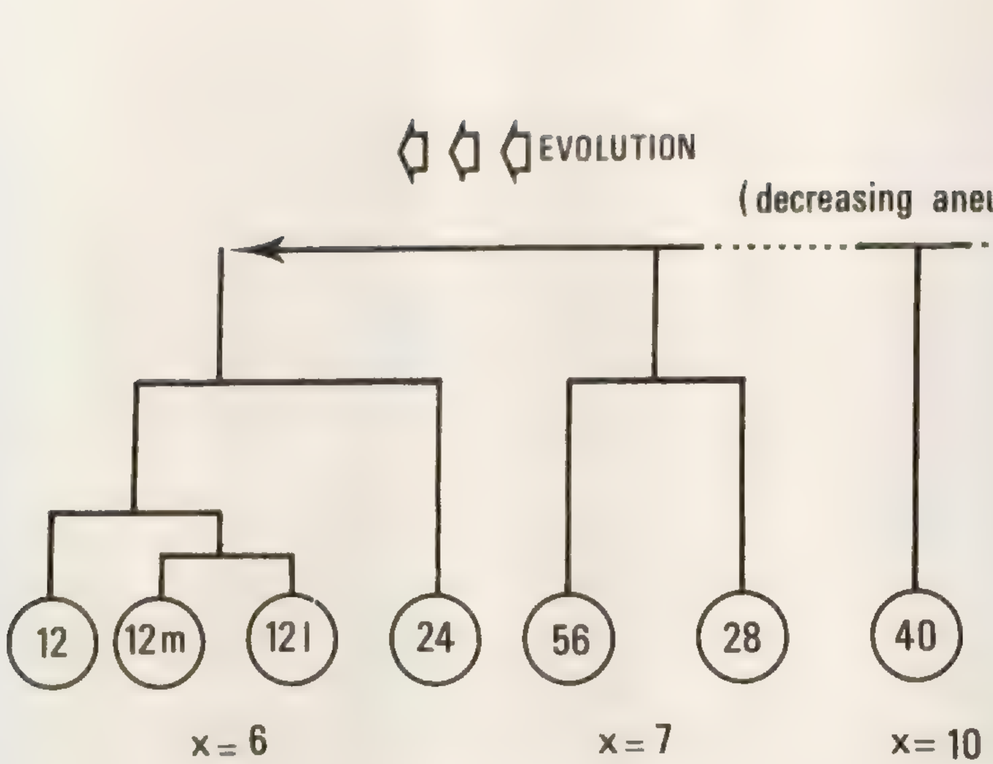
FIGURE 4. Deciduous branchlet and pistillate flower of *Phyllanthus odontadenius* ($2n = 24$), *P. magnificens* ($2n = 40$) and the two hybrids.—E, E'. Deciduous branchlet and ♀ flower of parent 24.—F, F'. Deciduous branchlet and ♀ flower of hybrid 24 × 40.—G, G'. Deciduous branchlet and ♀ flower of hybrid 40 × 24.—H, H'. Deciduous branchlet and ♀ flower of parent 40.

By analogy with what we observed in the *P. urinaria* complex, and by comparing the two dendrograms (Fig. 5), it appears that the taxa with $2n = 12$ are of the most recent phylogenetic origin. This assumes an aneuploid reduction from taxa with $x = 10$ (*P. magnificens*) to those with $x = 7$ and $x = 6$.

However, although there are some parallels in the diversification within the two complexes, there are also some differences. In the *P. urinaria* complex, it seems most logical to consider taxa with $2n = 50$ and $2n = 100$ as diploids and tetraploids based on a common basic number ($x = 25$). This number of $x = 25$ is most probably the result of an amphiploidization between species with $x = 12$ and $x = 13$.

In contrast, in the *P. odontadenius* complex there are several groups of taxa with different base numbers: diploid and tetraploid species with $x = 6$, tetraploid and octoploid with $x = 7$, and a tetraploid with $x = 10$ (*P. magnificens*), newly reported in this paper. This new basic number, reported for the first time in *Phyllanthus*, reinforces the hypothesis suggested by Webster (1967: 377) that the basic numbers of herbaceous *Phyllanthus* might form a descending series from $x = 13$ to $x = 12$, (. . .), (. . .), 9, 8, 7, 6. We can now almost complete this series, giving $x = 12$, (. . .), 10, 9, 8, 7, 6.

Strong chromosomally based crossing barriers observed by us in two complexes of herbaceous *Phyllanthus* (*P. odontadenius* and *P. urinaria*) between morphologically similar plants were not unique to this genus. This pattern is common in annual plants. Grant (1971) made the point with numerous examples. This is the case, for example,



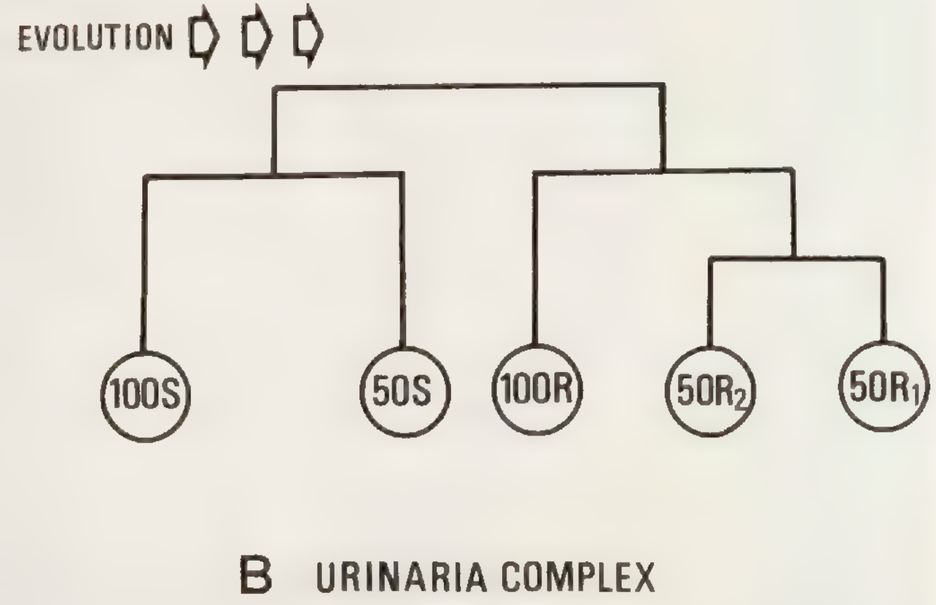


FIGURE 5. Dendrograms showing proposed relationships in the *Phyllanthus odontadenius* complex and *P. urinaria* complex.

in several genera of Compositae [*Madia*, *Layia* (Clausen, 1951), *Microseris* (Chambers, 1955), and *Helianthus* (Heiser et al., 1962)], in the genus *Gilia* (Polemoniaceae) (Grant, 1954), and in *Clarkia* (Onagraceae) (Lewis & Lewis, 1955).

In the Cruciferae we find the pattern exemplified by *Brassica* (Yarnell, 1956), in the Scrophulariaceae by *Collinsia* (Garber, 1960), in the Solanaceae by several annual sections of *Nicotiana* (Goodspeed, 1954), and in the Graminaceae it is displayed inter alia by *Bromus* sect. *Ceratochloa* (Hall, 1955).

Literature Cited

Belliard, J. & J. Besse. 1980. Etude du rôle des feuilles dans un phénomène d'incompatibilité entre deux taxons de *Phyllanthus odontadenius* Muell. Arg. Bull. Soc. Bot. France, 127, Lettres Bot. (1): 5–21.

Brunel, J. F. & J. Roux. 1981. *Phyllanthus* subsect. *Odontadenii* (Euphorbiaceae) au nord du fleuve Congo (Afrique de l'Ouest). Willdenowia 11: 69–89.

Chambers, K. L. 1955. A biosystematic study of the annual species of *Microseris*. Contrib. Dudley Herbarium (Stanford) 4: 207–312.

Clausen, J. 1951. Stages in the Evolution of Plant Species. Cornell Univ. Press, Ithaca, New York.

Garber, E. D. 1960. The genus *Collinsia* IX. Speciation and chromosome repatterning. Cytologia 25: 233–243.

Goodspeed, T. H. 1954. The genus *Nicotiana*. Chronica Botanica, Waltham, Massachusetts.

Grant, V. 1954. Genetic and taxonomic studies in *Gilia*. VI Interspecific relationships in the leafy-stemmed *Gilias*. Aliso 3: 35–49.

———. 1971. Plant Speciation. Columbia Univ. Press, New York.

Haicour, R. 1983. La variabilité de compatibilité entre divers taxons de *Phyllanthus urinaria* L. (Euphorbiacées): Mise en évidence et perspectives ouvertes pour son analyse. Bull. Soc. Bot. France 130, Lettres Bot. (3): 207–226.

———. 1984a. Eléments d'analyse de la structure des populations et de l'évolution d'une espèce rudérale pantropicale, *Phyllanthus urinaria* L. (Euphorbiaceae). 1. Etude du polymorphisme de l'entité *P. urinaria* et premier essai de classification. Bull. Mus. Nat. Hist. Nat. Paris, IV. 6 (sect. B, Adansonia 1): 63–74.

———. 1984b. Eléments d'analyse de la structure des populations et de l'évolution d'une espèce rudérale pantropicale *Phyllanthus urinaria* L. (Euphorbiaceae). 2. Etude de la variation génétique et de la traduction phénotypique. Bull. Mus. Nat. Hist. Nat. Paris, IV. 6 (sect. B, Adansonia 2): 157 191.

Hall, B. M. 1955. Genetic analysis of interspecific hybrids in the genus *Bromus*, section *Ceratochloa*. Genetics 40: 175–192.

Heiser, C. B., C. Martin & D. M. Smith. 1962. Species crosses in *Helianthus* I. Diploid species. Brittonia 14: 137–147.

Lewis, H. & M. Lewis. 1955. The genus *Clarkia*. Univ. Calif. Publ. Bot. 20: 241–392.

Monnier, M. 1973. Croissance et développement des embryons globulaires de *Capsella Bursa-pastoris* cultivés in vitro dans un milieu à base d'une nouvelle solution minérale. Bull. Soc. Bot. France, Mém., Coll. Morphologique, 179–194.

Rossignol, L., M. Rossignol & R. Haicour. 1987. A systematic revision of *Phyllanthus* subsection *Urinaria* (Euphorbiaceae). Amer. J. Bot. 74: 1853–1862.

Tran Ha, N. M. & L. Bancilhon-Rossignol. 1976. Premières données sur le mode de reproduction des *Phyllanthus* (Euphorbiacées) découlant d'une étude cytogénétique comparée de six taxons de *P. odontadenius* Muell. Arg. à garnitures chromosomiques différentes (2n = 12, 24, 28, 56). Rev. Cyt. Biol. Végét. 39: 201–234.

———, ——— & J. Belliard. 1976. Analyse morphologique et biométrique comparée de six taxons de *Phyllanthus odontadenius* Muell. Arg. à garnitures chromosomiques différentes (2n = 12, 24, 28, 56) et de leur descendance. Rev. Gen. Bot. 83: 269–310.

Webster, G. L. 1967. The genera of Euphorbiaceae in the southeastern United States. J. Arnold Arbor. 48: 304–430.

Yarnell, S. H. 1956. Cytogenetics of the vegetable crops. II. Crucifers. Bot. Rev. 22: 81–166.

EARLY EVOLUTION OF *DALECHAMPIA* (EUPHORBIACEAE): INSIGHTS FROM PHYLOGENY, BIOGEOGRAPHY, AND COMPARATIVE ECOLOGY[1]

W. Scott Armbruster[2]

Abstract

Dalechampia contains over 120 species and occurs throughout the lowland tropics of Asia, Africa, and the New World. Most species in both the Old and the New World secrete terpenoid resin from large glandlike aggregations of bractlets in the pseudanthial inflorescences (blossoms) and are pollinated by bees that collect resin for use in nest construction. Using comparative chemical, morphological, and ecological data and phylogenetic analyses, I attempt to ascertain the early evolutionary and biogeographic events that led to the present distribution of species, character states, and pollination systems throughout the tropics. Available evidence suggests the genus originated in western Gondwana or South America in the mid Cretaceous or early Tertiary, respectively, and spread throughout the tropics by the rafting of land masses, or by migration across higher latitudes when they had subtropical climates, or both. There is some evidence for two migrational events between the Old and New Worlds. The original pollination system may have involved pollination by pollen-collecting insects or by fragrance-collecting male euglossine bees. The origin of pollination by resin-collecting bees appears to have been a consequence of a preadaptation (exaptation): the earliest *Dalechampia* apparently used triterpene resins to defend flower parts against attack by herbivores and/or microbes, and resin secondarily assumed the role of pollinator reward. The mutualistic relationship with resin-collecting bees may have originated independently in the Old and New Worlds.

Trans-oceanic disjunctions of similar plant species have intrigued plant biologists since the earliest botanical explorers began to report them. We have long wondered how such disjunctions arose, when and how dispersal occurred, and how populations evolved in isolation from each other. Disjunctions create natural evolutionary experiments in which two or more populations of similar genetic stock evolve independently in response to local environmental conditions. An interesting challenge is to unravel the history of disjunctions and reconstruct the evolutionary events that have occurred since the isolation of plant populations.

Research on this topic has rarely proceeded beyond the phase of description of the distributions of disjunct sister taxa and their taxonomic relationships. This is because research on historical phenomena, especially those as ancient as the events creating trans-oceanic disjunctions, is extremely difficult, and until recently required a detailed fossil record. The development of powerful computer-assisted methods of phylogeny reconstruction, however, now makes it realistic to attempt retrospective analysis of ancient biogeographic and evolutionary processes in the absence of a fossil record (see Donoghue, 1989). The field of vicariance biogeography represents one such approach in its attempt to use analyses of phylogenetic relationships of several independent taxa as an aid to ascertaining the processes that affected the distribution of those taxa (see review in Humphries & Parenti, 1986).

In the present paper I consider four questions about the early evolutionary and biogeographic events that affected the members of the pantropical euphorb genus *Dalechampia*: (1) Where and when did the genus originate? (2) What series of events led to the present geographical distribution of species, character states, and pollination systems? (3) What was the original pollination system in the

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genus, and how did the early diversification of pollination systems occur? (4) How, when, and where did the novel mutualism with resin-collecting bees arise? Using the cladistic method of phylogeny reconstruction, I develop explicit hypotheses addressing the four historical questions. I evaluate the hypotheses by considering independent data on the relationships between the plants and their herbivores and pollinators.

Natural History and Distribution of *Dalechampia*

Dalechampia is distinctive within the Euphorbiaceae: the ca. 120 species have pseudanthial inflorescences (blossoms) in which usually 3 pistillate flowers and usually 4–16 staminate flowers are united into subterminal and terminal cymules, respectively. Close examination of the *Dalechampia* inflorescence, however, indicates that its arrangement is probably homologous to that of the inflorescences of *Tragia* and *Plukenetia* (although in these taxa the inflorescences are not pseudanthial, i.e., do not function as single pollination units as in *Dalechampia*) (Webster & Webster, 1972). These three taxa are also similar in habit. Unlike most other euphorbs, *Tragia* and *Plukenetia* comprise viny species and *Dalechampia* comprises mostly viny species. *Tragia* and *Dalechampia* are also similar in having urticating, crystaliferous trichomes of virtually identical morphology (Webster & Webster, 1972). For these reasons, Webster (1994) has recently proposed that *Dalechampia* be included in tribe Plukenetieae (with *Tragia* and *Plukenetia*) rather than isolated in its own tribe as in earlier treatments (e.g., Webster, 1975). The striking similarities among these three genera and their inferred close relationship make it possible to use, with considerable confidence, *Tragia* and *Plukenetia* as candidate outgroups in the phylogenetic analyses described below.

Despite the relatively uniform blossom morphology in *Dalechampia*, there is considerable variation in the reproductive biology. Most species in both the Paleotropics and Neotropics offer resin as a pollinator reward and are pollinated by female or worker bees that collect resin from a variety of plant sources and use it in nest construction (Cammerloher, 1931; Armbruster & Webster, 1979; Armbruster, 1984; Armbruster & Mziray, 1987). The resin is secreted by a cluster of modified bractlets (the "resin gland") associated with the staminate flowers (Webster & Webster, 1972). About a dozen species in the New World offer fragrances as a pollinator reward and are pollinated by fragrance-collecting male euglossine bees (Apidae: Euglossini) (Armbruster & Webster, 1979; Armbruster et al., 1989; Armbruster et al., 1992). These bees apparently use fragrances as precursors in the biosynthesis of sex pheromones (Dressler, 1982; Whitten et al., 1989). Several species in the Neotropics and in Madagascar appear to produce no reward for pollinators other than pollen; these species are pollinated by pollen-collecting bees and beetles (Armbruster et al., 1993).

Species of *Dalechampia* are found throughout the lowland tropics of Asia, Africa, and the New World, although the greatest diversity is expressed in South America (Fig. 1). Species bearing resin glands (and pollinated by resin-collecting bees) are by far the most widespread; they occur in every major region where *Dalechampia* is found, except Madagascar. Those species pollinated by male euglossine bees are necessarily restricted to the Neotropics, because euglossines are endemic to the New World. Species lacking the resin gland and pollinated by pollen-seeking insects are most diverse in Madagascar, but are also found in northern South America and southern Central America.

Several authors have concluded that the glandless species found in Madagascar form the most basal species group in the genus (Michaelis, 1924; Magin, 1987), while Webster & Armbruster (1991) considered the glandless species of northern South America (sect. *Rhopalostylis*) to form probably the most basal group. It is possible that the Madagascan and South American glandless species, which share numerous characteristics, form a single basal monophyletic or paraphyletic cluster of species. This raises the possibility that *Dalechampia* has a complex biogeographic history, with multiple migrations among the continents and independent evolution of the mutualism with resin-collecting bees in the Old and New World tropics (Armbruster & Mziray, 1987). Alternatively, if the resemblance between Madagascan species and members of section *Rhopalostylis* is the result of homoplasy (character convergence and/or reversals), there may be no reason to reject a very simple biogeographic history involving an origin in the New or the Old World, followed by dispersal to the other hemisphere.

Armbruster & Mziray (1987) proposed four alternative dispersal hypotheses that could explain the present distribution of *Dalechampia* species: (1) recent long-distance dispersal of species among continents, (2) migration across mid- to high-latitude land bridges during the Tertiary, when these latitudes had subtropical climates, (3) a nearly continuous western Gondwanan distribution in the mid

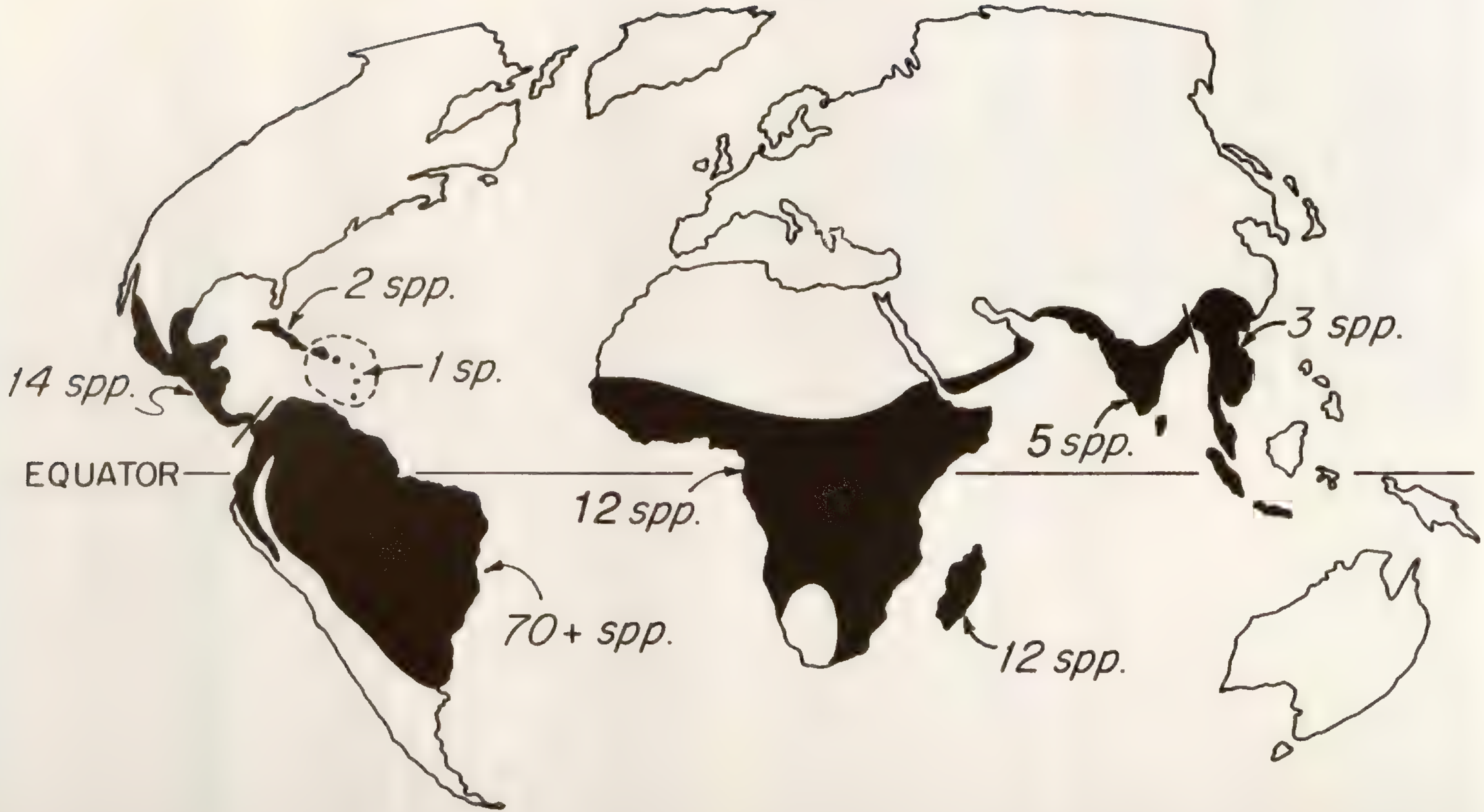

FIGURE 1. Approximate distribution and number of species of *Dalechampia* in the Paleo- and Neotropics.

to late Cretaceous disrupted by subsequent continental drift, and (4) distribution of primitive *Dalechampia* in South America, Africa, and Madagascar by continental drift, followed by extinction of primitive species in Africa and a second migration (either by long-distance dispersal or migration via higher latitudes) of more derived species between South America, Africa, and Asia. Circumstantial evidence they provided supported the second, third, and fourth hypotheses, but not the first. They did not attempt to identify the site of origin of the genus nor the direction dispersal events. The purpose of the present study is to use phylogenetic analyses of the New and Old World species to refine these biogeographic hypotheses and specify possible sites of origin of the genus, directions of dispersal, pollination ecology of the earliest species, and the site(s) of origin of the novel mutualism with resin-collecting bees.

Phylogenetic Inference

Methods

To reconstruct phylogenetic relationships among Old and New World species of *Dalechampia*, I conducted cladistic analyses on a data set of 46 morphological characters (Table 1) from 25 neotropical, 4 African, and 3 Madagascan species of *Dalechampia* and representatives of two sister genera, *Tragia* and *Plukenetia*, to serve as possible outgroups (Appendix). The species of *Dalechampia* were chosen to represent the major species groups in the genus. I used the heuristics algorithm of PAUP 3.0 (see Swofford, 1993) on a Macintosh microcomputer to find the shortest trees. In this analysis ancestral states were not specified (i.e., characters were not polarized). Instead, PAUP determined the ancestral states through global parsimony (Maddison et al., 1984), selecting the more parsimonious of the two sister taxa to be the outgroup. I used MacClade 3.0 (see Maddison & Maddison, 1992) to explore alternate tree topologies, analyze character evolution, assess tree congruence with alternative biogeographic hypotheses, and produce graphics.

After an initial run with the full set of taxa (including the sister genera), I eliminated all but one member of each stable, well defined clade of neotropical species and all but two of the very similar taxa in the paraphyletic section *Rhopalostylis*. This reduced the number of New World taxa to 11 and Old World taxa to 4. The decreased number of taxa greatly reduced PAUP run time on the computer. To further reduce run times the results of the initial cladistic analysis were used to polarize characters and specify ancestral character states, and the outgroups were eliminated. These procedures left unaltered the relative positions of Old and New World taxa.

Iterative cladistic runs were conducted to determine the sensitivity of cladistic results to initial assumptions about character reversibility (Table 2). I varied the assumption of character reversibility (reversible vs. irreversible between plesiomorphic [primitive] and apomorphic [derived] states) for each of three selected characters, and in all possible combinations of the three characters.

I then examined each of the numerous maximally parsimonious trees to determine the simplest biogeographic and evolutionary scenarios that could explain the distribution of taxa, character states, and pollination systems and were consistent with the tree. This was accomplished by manually mapping distribution and pollination ecology data onto each tree using the parsimony assumption (see Maddison & Maddison, 1992).

Results

When all characters were assumed reversible, cladistic analysis of the set of 34 taxa yielded 436 equally parsimonious trees (120 steps, consistency index [CI] = 0.47). The large number of equally parsimonious trees reflects instability in the placement of a few similar taxa (Fig. 2). The gland characteristics, pollination ecology, and geographical distribution of the various ancestral taxa (nodes of the tree) were inferred by parsimony from the distribution of these characteristics across the extant taxa (Maddison & Maddison, 1992). "Mapping" of characteristics onto the consensus tree allowed inference of the history of these ecological and biogeographic features. Despite the abundance of equally parsimonious trees, the evolutionary and biogeographic implications of this cladistic analysis generally supported Hypothesis 1 (Table 3): *Dalechampia* originated in the Neotropics or western Gondwana, and the earliest species were initially pollinated by either fragrance-collecting male euglossines or pollen-collecting insects (Figs. 2, 3). *Dalechampia* evolved a mutualistic (pollination) relationship with resin-collecting bees in the Neotropics, and relatively recently in the genus's evolutionary history a resin-reward species colonized Africa. More recently, there occurred a migration from Africa to Madagascar. The colonists of Madagascar apparently evolved pollination by pollen-collecting bees and/or beetles just after they colonized Madagascar.

Cladistic analysis of the reduced set of taxa

TABLE 1. Characters and character states used in phylogenetic analyses. The "0" character state is the ancestral condition, as determined by global-parsimony outgroup analysis. * indicates character was not used in the phylogenetic analysis.

1. Nature of proximal involucral bract: 0 = stipuliform; 1 = involucral.
2. Nature of distal involucral bract: 0 = stipuliform; 1 = involucral.
3. Position of proximal involucral bract: 0 = separated from pistillate cymule; 1 = adjacent to pistillate cymule.
4. Stipels on proximal involucral bract: 0 = present; 1 = absent.
5. Number of basal veins of involucral bracts: 0 = 3; 1 = 5 or more.
6. Color of involucral bracts: 0 = white to pale green; 1 = pink; 2 = yellow; 3 = brown; 4 = deep green.
7. Shape of base of involucral bracts: 0 = cuneate; 1 = cordate.
8. Shape of tip of involucral bracts: 0 = entire, acute; 1 = lobed.
9. Persistence of involucral bracts: 0 = deciduous shortly after anthesis; 1 = persistent into fruiting.
10. Number of pistillate sepals: 0 = 5–6; 1 = >7; 2 = 4.
11. Margins of pistillate sepals: 0 = entire; 1 = lobed.
12. Presence of distal pistillate involucellar bractlets: 0 = present; 1 = absent.
13. Size of distal pistillate involucellar bractlets: 0 = small, stipuliform; 1 = large, enveloping.
14. Shape of pistillate sepals (excluding lobes): 0 = ovate; 1 = linear.
15. Style shape: 0 = cylindrical to slightly dilated at tip; 1 = clavate; 2 = strongly dilated at tip; 3 = umbraculiform; 4 = deeply lobed.
16. Number of stamens: 0 = 5–10; 1 = >11.
17. Fusion of staminate involucellar bracts: 0 = free; 1 = connate.
18. Symmetry of staminate pleiochasial arms: 0 = decussate; 1 = bilateral.
19. Number of staminate pleiochasial arms: 0 = 4; 1 = 5.
20. Arrangement of staminate bractlets: 0 = symmetrically distributed; 1 = clustered into "gland."
21. Tip of staminate bractlets: 0 = acute; 1 = truncate.
22. Margins of staminate bractlets: 0 = entire; 1 = laciniate.
23. Resin secretion by staminate bractlets: 0 = absent; 1 = present.
24. Resin color: 0 = clear, whitish; 1 = yellow, orange; 2 = maroon; 3 = blue.
25. Staminate sepal color: 0 = green to whitish; 1 = pink.
26. Stigma color: 0 = pale to deep green; 1 = pink to maroon.
27. Habit: 0 = vine; 1 = shrub.
28. Relative petiole length: 0 = >¼ limb length; 1 = <1/10 limb length.
29. Leaf shape: 0 = simple, entire; 1 = compound; 2 = simple, 3–5-lobed.
30. Leaf venation: 0 = palmate; 1 = pinnate.
31. Leaf stipules: 0 = stipuliform; 1 = foliose.
32. Involucral bract stipules: 0 = stipuliform; 1 = foliose.

TABLE 1. Continued.

33. Pollen shape: 0 = prolate; 1 = subspherical.
34. Seed surface: 0 = smooth; 1 = rugulose; 2 = tuberculate.
35. Seed shape: 0 = round; 1 = 3-angled; 2 = lenticular; 3 = slightly flattened.
36. Petiole of proximal involucral bract: 0 = present; 1 = absent.
37. Pollen exine: 0 = reticulate; 1 = psilate.
38. Relative size of pistillate sepals in fruit: 0 = <½ capsule length; 1 = approximately capsule length; 2 = fully enveloping capsule.
39. Stinging crystalliferous trichomes: 0 = absent; 1 = present.
40. Number of carpels: 0 = 3; 1 = 4.
41. Number of sterile arms in staminate pleiochasium: 0 = 0; 1 = 1; 2 = 2.
*42. Pollination: 0 = pollen-collecting bees (*Trigona* workers) or cetoniine beetles; 1 = resin-collecting bees (*Hypanthidium* females, *Trigona* workers, *Euglossa*, *Eulaema*, and *Eufriesea* females); 2 = fragrance-collecting male euglossine bees (*Euglossa*, *Eulaema*, *Eufriesea*).
43. Fusion of distal pistillate bractlets: 0 = free; 1 = connate.
44. Presence of leaf stipels: 0 = absent; 1 = present.
45. Leaf nectary: 0 = absent; 1 = present.
46. Inflorescence condensation: 0 = not condensed; 1 = highly condensed.
47. Expression of leaf stipules: 0 = well developed; 1 = reduced to absent.

yielded 50 equally parsimonious trees (70 steps, CI = 0.61). All of these were consistent with the biogeographical and evolutionary conclusions drawn from the analysis of the full set of taxa (Table 2, Fig. 4).

How reasonable is it to assume that all characters can evolve forward and backward repeatedly? Is it realistic to expect that structures are regained as easily (frequently) as they are lost? For certain characters at least, the answer may be "no." Upon reflection I became uncomfortable with allowing characters 17 (fusion of male involucel), 20 (presence of a "resin gland"), and 41 (presence of sterile pleiochasial arms) to revert to the plesiomorphic state as they do in all 436 (first analysis) and 50 (second analysis) maximally parsimonious trees. It seemed unlikely (although not impossible) from a developmental perspective for these characters to revert from the derived (apomorphic) condition back to the primitive (plesiomorphic) condition. For example, consider character 17: whether the involucellar bracts of the staminate subinflorescence (pleiochasium) are free, each subtending a pleiochasial arm, or are connate (fused). Based on outgroup comparisons, the former state appear to be plesiomorphic and the latter derived. Al-

TABLE 2. Consequences of varying initial assumptions of reversibility of characters upon the biogeographic/evolutionary conclusions drawn from the most parsimonious trees obtained by cladistic analysis of the reduced list of *Dalechampia* taxa. Numbers indicate biogeographic/evolutionary hypothesis(es) with which the most parsimonious trees were consistent (see Table 3). Numbers in parentheses indicate the proportion of maximally parsimonious trees consistent with each hypothesis.

Character assumed irreversible	Alone	In combination with character 20	41	17, 20
17. Fusion of staminate bracts	2 (96%)[1] 4 (3%) 3, 4 (1%)	3 (60%)[2] 2, 3 (33%) 5 (4%) 2, 5 (4%)	3 (100%)[3]	—
20. Presence of resin gland or its vestige	3 (60%)[2] 3, 5 (33%) 5 (4%) 2, 5 (4%)	—	3 (100%)[3]	—
41. Presence of sterile arms in staminate pleiochasium	3 (100%)[3]	—	—	3 (100%)[3]
None	1 (100%)[4]	—	—	—

[1] N = 252 equally parsimonious trees.
[2] N = 114 equally parsimonious trees.
[3] N = 42 equally parsimonious trees.
[4] N = 50 equally parsimonious trees.

though the shift to the connate condition may not be expected to occur frequently, it seems even less likely that the connate involucre would split up into the "correct" number of bractlets, in the arrangement that recreates the original relationship between bracts and pleiochasial arms. Thus if there is homoplasy in this character, it seems more likely to reflect convergence than reversal.

The assumption of irreversibility was applied to each of these characters in turn and in all possible combinations. The cladograms from the seven different runs generated hypotheses 3, 2, 5, and 4 in order of frequency (Tables 2, 3). By far the most commonly supported hypothesis was H_3, with H_2 a distant second. For example, the assumption that a sterile pleiochasial arm cannot readily become fertile again resulted in 42 equally parsimonious trees that all support H_3: *Dalechampia* originated in the Neotropics or western Gondwana, a glandless lineage colonized the Paleotropics (by the breakup of Gondwana or migration via higher latitudes), mutualisms with resin-collecting pollinators evolved separately in the Old and New Worlds, followed by recolonization of the Neotropics by Old World gland-bearing (resin-producing) species, extinction of the glandless species from most of Africa, and their persistence in Madagascar (Fig. 5).

The assumption that the fusion of staminate bracts is irreversible, when taken alone, produced 252 maximally parsimonious trees, 96% of which supported H_2 (Table 2). In this hypothesis, *Dalechampia* originated in the Neotropics or western Gondwana, a glandless stock colonized the Paleotropics (by the breakup of Gondwana or migration via higher latitudes), the mutualism with resin-collecting bees originated in the Neotropics, followed by one or more additional colonizations of the Old World from the New by gland-bearing (resin-producing) species (Fig. 6).

All other assumptions and combinations of assumptions of irreversibility of characters yielded shortest trees that supported H_3 either all or most of the time (Table 2). Thus it appears that the most likely biogeographic/evolutionary hypotheses are H_1, H_3, and H_2. Which of these one favors depends not only on whether one assumes characters in general are reversible or irreversible, but also on which particular character or combination of characters are assumed irreversible. Assumptions about the irreversibility of certain characters have stronger effects on biogeographic conclusions than others. That is, assumptions of irreversibility of certain characters appear to be dominant, in their effects, over others. The "pecking order" apparent in Table 2 is Character 41 > Character 20 > Character 17.

All of the phylogenetic hypotheses derived from the cladistic analyses lead to two basic conclusions. (1) *Dalechampia* originated in the Neotropics or

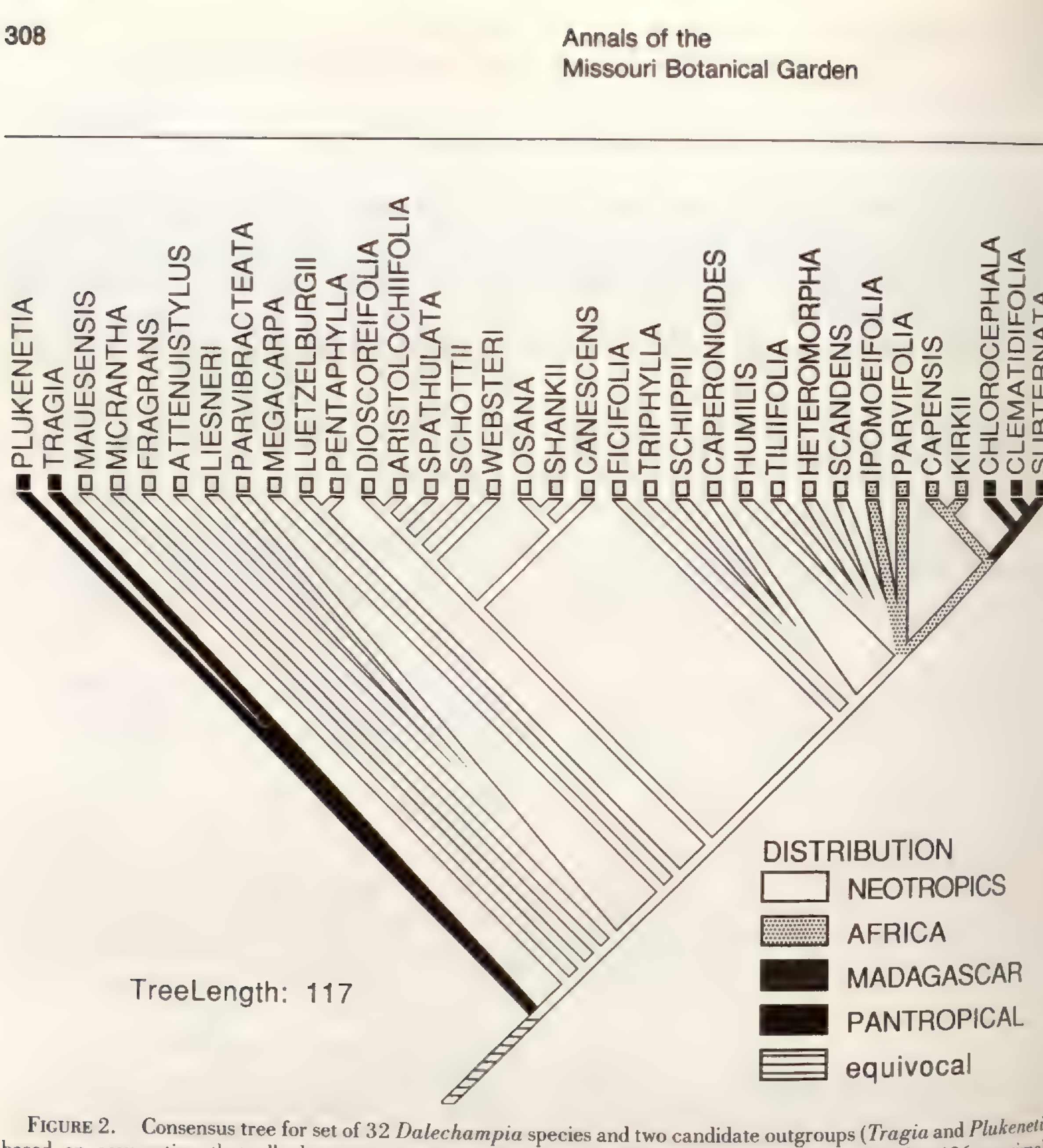

FIGURE 2. Consensus tree for set of 32 *Dalechampia* species and two candidate outgroups (*Tragia* and *Plukenetia*) based on assumption that all characters are reversible. Taxa with unstable arrangements in the 436 maximally parsimonious trees are indicated by polytomies (points of branching of more than two taxa).

western Gondwana. (2) The earliest species were pollinated by pollen-collecting insects or fragrance-collecting male euglossine bees. Uncertainty remains as to when and in which direction dispersal between the Old and New Worlds occurred.

TESTS OF HYPOTHESES

There are several sources of independent data that could be used to evaluate the biogeographic/evolutionary hypotheses generated by phylogenetic analyses. These include information on the relationships among specialist insect herbivores on Old and New World *Dalechampia*, the chemical defense systems that *Dalechampia* uses against herbivores, details of pollination biology of Old and New World *Dalechampia*, and morphological details of the resin gland of Old and New World species.

SPECIALIST HERBIVORES ON *DALECHAMPIA*

There are several genera of nymphalid butterflies whose larvae appear to be specialist folivores on New and Old World *Dalechampia*. The phylogenetic relationships among the New and Old World butterflies may give us some clues about the history of their and their host plants' migrations among the Neotropics and Paleotropics.

Assuming that specialist *Dalechampia* folivores feed only on *Dalechampia*, one can make several specific predictions about the phylogenetic relationships between those of the New and Old Worlds, depending on the biogeographic scenario used to account for their present distribution. (1) If the initial dispersal of *Dalechampia* from the New World to the Old occurred by long-distance dispersal after the continents achieved close to their present positions, the butterfly herbivores in the

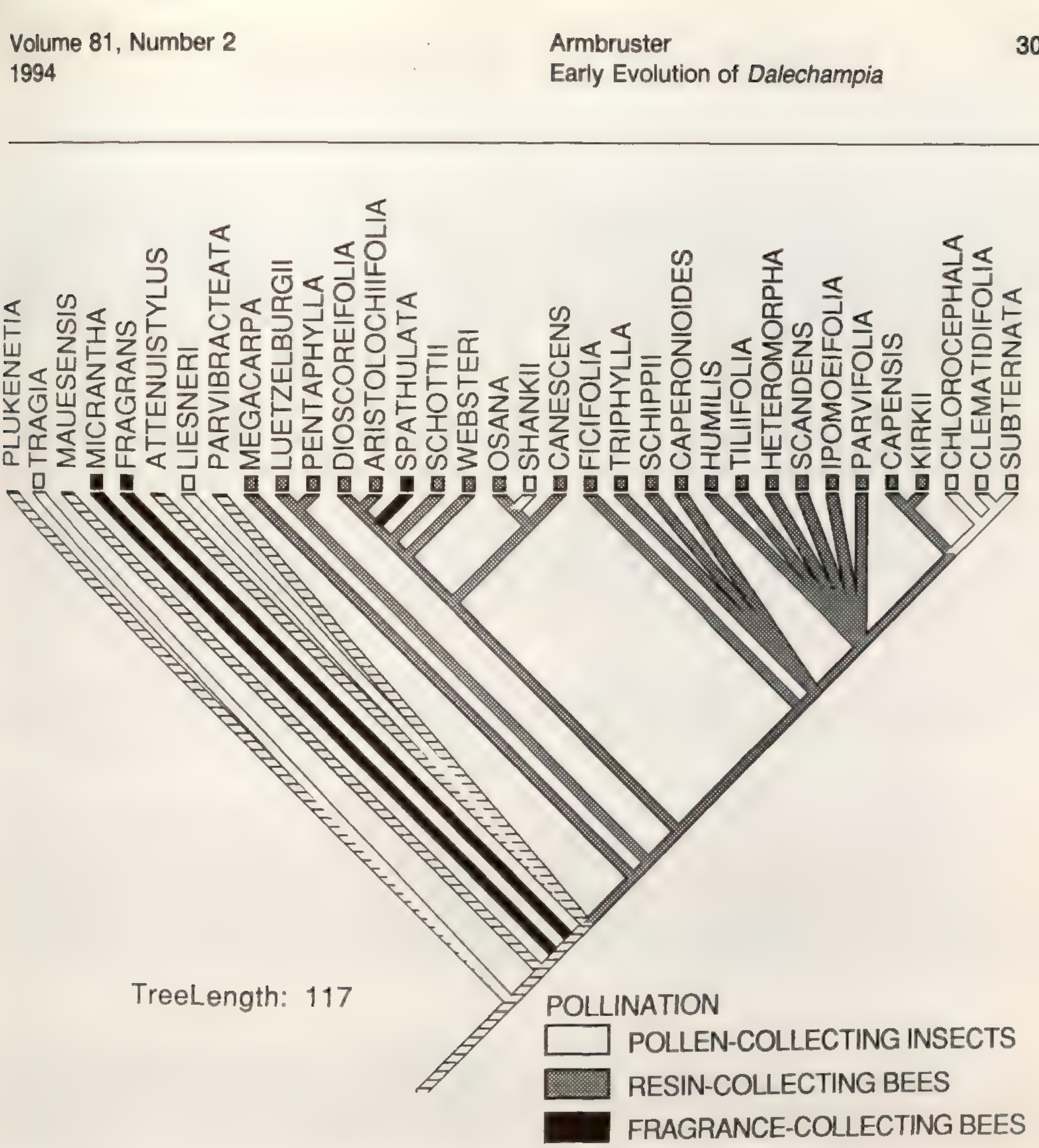

FIGURE 3. Same cladogram as is in Figure 2, with pollination systems mapped onto the branches.

Old and New Worlds should be completely unrelated. This is because it is extremely unlikely that both host plant and herbivore would have become established in the Paleotropics by long-distance dispersal from the New World, and the Old World herbivore fauna would more likely be the result of members of the local butterfly fauna evolving to feed on *Dalechampia*. (2) If the initial dispersal from the New World to the Old occurred by migration of a semi-continuous population stretching across North America and Europe or Asia in the early to mid Tertiary, when these continents had subtropical climates, the butterfly herbivores in the Old World should be closely related sister taxa of the New World species. This is because a semi-continuous population of host plants across the higher latitudes should have allowed a semi-continuous population of the herbivores to also disperse into the Old World. (3) If the initial dispersal from the New World to the Old occurred by a continuous population being split into two or more populations by the rafting apart of the continents (the breakup of Gondwana) in the Cretaceous, the Old and New World herbivores should again be sister taxa, but not as closely related as in the second scenario.

There is some ecological information available on butterfly herbivores that feed on *Dalechampia* (Table 4; see Armbruster, 1983; Armbruster & Mziray, 1987; DeVries, 1987). Unfortunately there is not yet detailed information available on their phylogenetic relationships. The systematic (Table 4) and phylogenetic information that is available indicates a close phylogenetic relationship between Old and New World taxa, possibly forming two

TABLE 3. Five most parsimonious biogeographic hypotheses derived from the cladistic analyses under varying assumptions about character reversibility.

H_1.	The genus and the resin-collection mutualism originated in the New World, with a subsequent migration to the Old World from the New and the loss of the resin-collection mutualism in Madagascan taxa.
H_2.	The genus originated in the New World or western Gondwana; an initial migration (or rafting) to the Old World from the New was followed by the evolution of the resin-collection mutualism in the New World, and then by a second migration to the Old World by gland-bearing species.
H_3.	The genus originated in the New World or western Gondwana; an initial migration (or rafting) to the Old World was followed by the independent evolution of the resin-collection mutualism in Old and New Worlds, followed by a migration of gland-bearing species to the New World from the Old.
H_4.	The genus and the resin-collection mutualism originated in the New World, followed by a migration of gland-bearing species to the Old World, loss of the mutualism in Madagascar, and finally recolonization of the New World by gland-bearing species.
H_5.	The genus and the resin-collection mutualism originated in the New World, followed by two or more migrations of gland-bearing species to the Old World and subsequent recolonization of the New World by gland-bearing species.

groups with vicariant genera in both areas (Jenkins, unpublished manuscript; Armbruster & Mziray, 1987; Otero, 1990; Ackery, 1988). This observation generally supports the predictions of the hypotheses of early *Dalechampia* "migration" by continental drift and migration in the Tertiary via higher latitudes. It does not support the hypothesis of recent long-distance dispersal (see Armbruster & Mziray, 1987, for additional discussion). Thus the evidence from the relationship among the lepidopteran herbivores of the Old and New Worlds supports the hypotheses that show a fairly early colonization of the Old World from the New.

The observation that many of the lepidopterans that feed on *Dalechampia* may sometimes also feed on *Tragia* (Table 4), however, raises another possibility. It is possible that *Tragia* and its herbivores achieved a pantropical distribution prior to *Dalechampia*. If this were true, then the lepidopterans now specializing on *Dalechampia* in the Old World could be derived from *Tragia*-feeding ancestors. In this case phylogenetic relationships among lepidopteran herbivores may yield insights into the biogeographic history of *Tragia*, but not of *Dalechampia*.

EVOLUTION OF THE RESIN REWARD SYSTEM

How likely is it that an unusual pollination system such as pollination by resin-collecting bees could have originated more than once within *Dalechampia*? Elsewhere in the plant kingdom it has apparently originated only one other time, in *Clusia* (Guttiferae) (Armbruster, 1984). Therefore, it seems at first highly unlikely that pollination by resin-collecting bees would have arisen multiple times in the genus. Any biogeographic scenario invoking this would also seem improbable. Consideration of how the system arose, however, makes multiple origins of the relationship seem more probable.

TABLE 4. Provisional phylogenetic classification and host-plant associations of lepidopteran herbivores feeding on *Dalechampia* and related genera. Systematic relationships and host plant information from Jenkins (unpublished manuscript), Armbruster & Mziray (1987), Ackery (1988), Otero (1990), and D. Lees (unpublished data).

Neotropics	Paleotropics
Nymphalidae	
Subfamily Eurytelinae	
Tribe Neptini	
	Neptis (T[1], A, others)
Tribe Eurytelini	
Biblis (T)	*Byblia* (D, T, P)
Mestra (T, D)	*Mesoxantha* (T)
	Neptidopsis (D, T)
	Ariadne (T, R, D, Te, Ac)
	Eurytela (T, R, D, Te)
Tribe Epicaliini	
Hamadryas (D, T)	*Sallya* (D, T, others)
Ectima (D)	
Panacea (D??)	
Batesia (D??)	
Catonephele (A, D, V)	
Myscelia (D, Ad)	
Nessaea (P, A)	
Tribe Dynamini	
Dynamine (D, T)	

[1] Abbreviations for host plants: A = *Alchornia*, Ac = *Acalypha*, Ad = *Adelia*, D = *Dalechampia*, P = *Plukenetia*, R = *Ricinus*, T = *Tragia*, Te = *Tetracarpium*, V = *Veconcibea*.

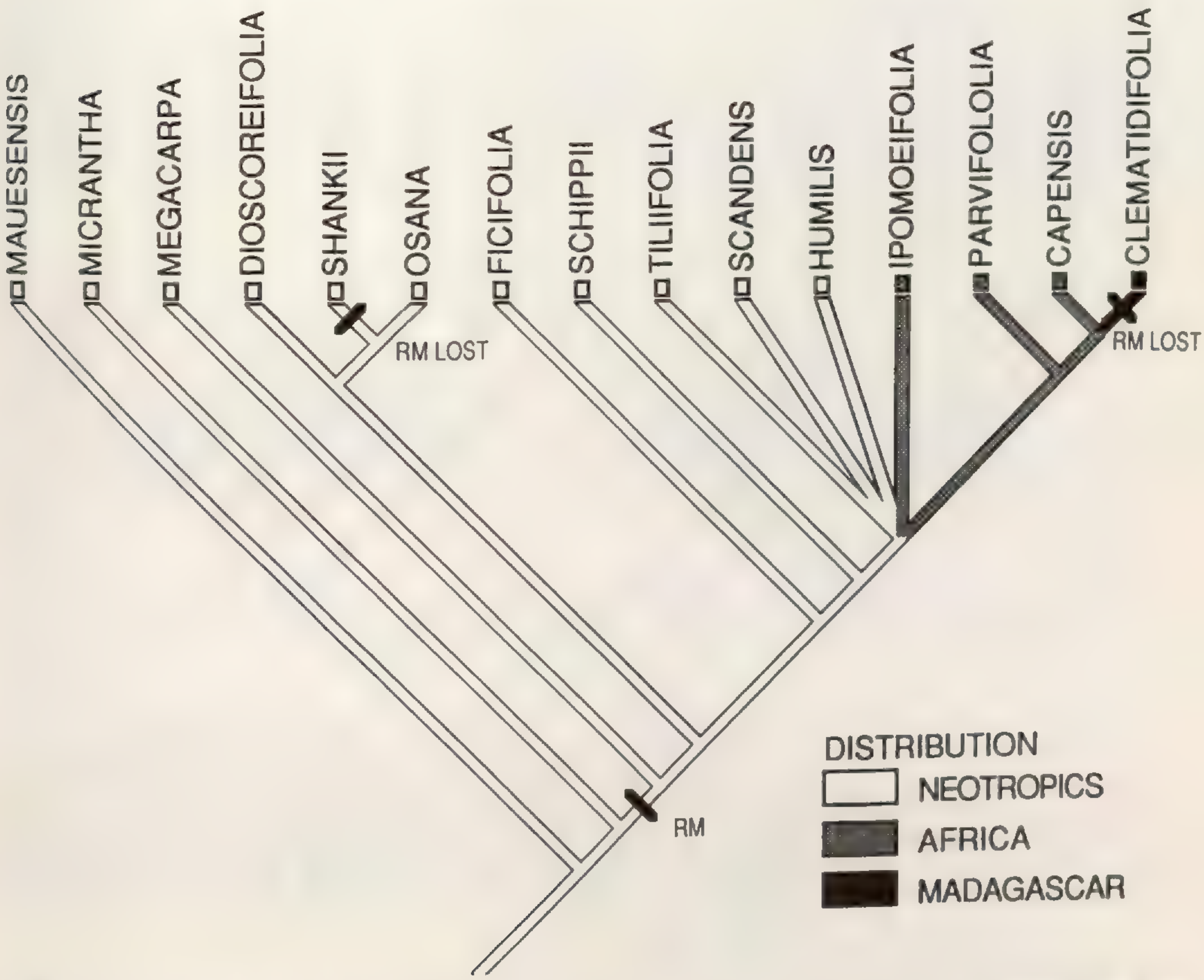

FIGURE 4. Consensus tree for the simplified set of taxa, assuming that all characters are reversible. The figure shows the species distribution mapped onto the cladogram and origins of the mutualism with resin-collecting bees ("resin mutualism" = RM). Taxa with unstable arrangements in the 50 maximally parsimonious trees are indicated by polytomies.

In all *Dalechampia* species that reward pollinating bees with triterpenoid resins, the secretory bractlets are clustered into a glandlike structure in the staminate subinflorescence. Comparative morphological studies of gland-bearing and non-gland-bearing species show that the bractlets of the gland are homologous to those that subtend the staminate flowers (and cover them in bud) in glandless species (Armbruster, unpublished obs.). The bractlets also secrete the same mixture of oxygenated triterpenes, even though the compounds play no role in pollination. These bractlets and their resinous secretions would instead appear to play a role in defending the staminate flowers from depredation by herbivorous insects or microbes. Also consistent with this idea is that some of the same compounds are also secreted by glands along the margins of young leaves, stipules, and/or sepals of many *Dalechampia* species, where they appear to play a role in defending those parts from herbivores (Armbruster, Howard & Debevec, unpublished data).

Species of *Dalechampia* identified in cladistic analyses as diverging early in the evolution of the genus do not use resin-collecting bees as pollinators, although they do produce resins from inflorescence bractlets. Character mapping indicates that the common ancestor of the rest of the genus also had this feature. This suggests that resin secretion in the genus first arose as a way of protecting reproductive tissues from attack by insect herbivores or microbes. Its presence in the inflorescence set the stage for resin-collecting bees to visit flowers to collect the resin for nest construction. These bees secondarily assumed the role of pollinators. The plant, in response, evolved higher rates of resin secretion, and the bractlets became organized into a gland from which the resin could be collected more efficiently. Thus the resin reward system probably evolved from a preadaptation (exaptation). Because the preadaptation was apparently "in place" very early in the evolution of the genus, it was probably present in the first *Dalechampia*

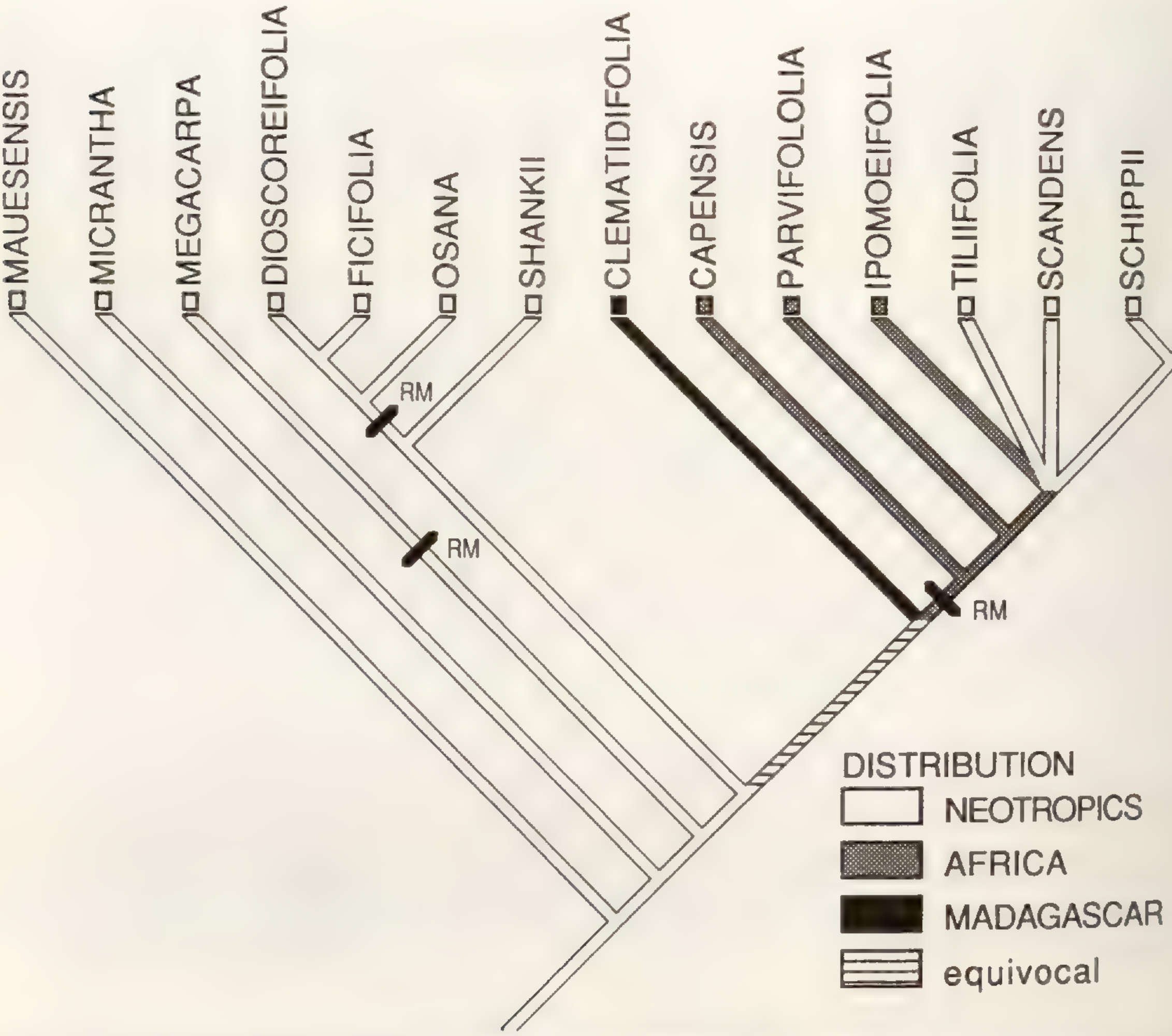

FIGURE 5. Consensus tree for the simplified set of taxa, assuming that all characters are reversible except character 41 (see Table 2), which was assumed irreversible. The figure shows the species distribution mapped onto the cladogram and origins of the mutualism with resin-collecting bees ("resin mutualism" = RM). Taxa with unstable arrangements in the 42 maximally parsimonious trees are indicated by polytomies.

to arrive in the Old World, as well as in the New World species. This is confirmed by the secretion of "defense" (non-reward) resins by many of the Madagascan species as well as several members of section *Rhopalostylis*. Thus the stage would have been set similarly in both the Paleotropics and Neotropics for the evolution of the mutualism with resin-collecting bees. Resin-collecting bees were probably already present in both the Paleo- and Neotropics (Michener, 1979). It thus seems not so unlikely that the resin-collecting mutualism might have originated independently in both places.

Another observation is consistent with two separate origins of the resin gland and resin-reward system. If the resin gland originated independently more than once, we might expect to see subtle differences in the structure of the gland. If the resin glands throughout the genus were of identical structure, it would suggest a single origin of the gland. There are actually two distinct kinds of resin gland. Members of sections *Dioscoreifoliae* and *Cremophyllum* have resin glands composed of a single concentric whorl of resiniferous bractlets derived from three pleiochasial arms. The gland-bearing species of the Old World and most of the more derived species of the New World have resin glands composed of two rows of nearly parallel platelike bractlets which are apparently derived from four pleiochasial arms. The two forms of gland are consistent with two origins of the resin gland. The distribution of the two gland types is consistent with the phylogeny that supports biogeographic Hypothesis 3: one migration to the Old World, a separate origin of the resin gland in the Old and New Worlds, followed by a recolonization of the New World by species bearing the Old World gland type (Fig. 5).

There are two final aspects of the pollination ecology that may have bearing on our biogeographic hypotheses. First, if *Dalechampia* had tight relationships with resin-collecting pollinators prior to its colonization of the Old World (as it apparently

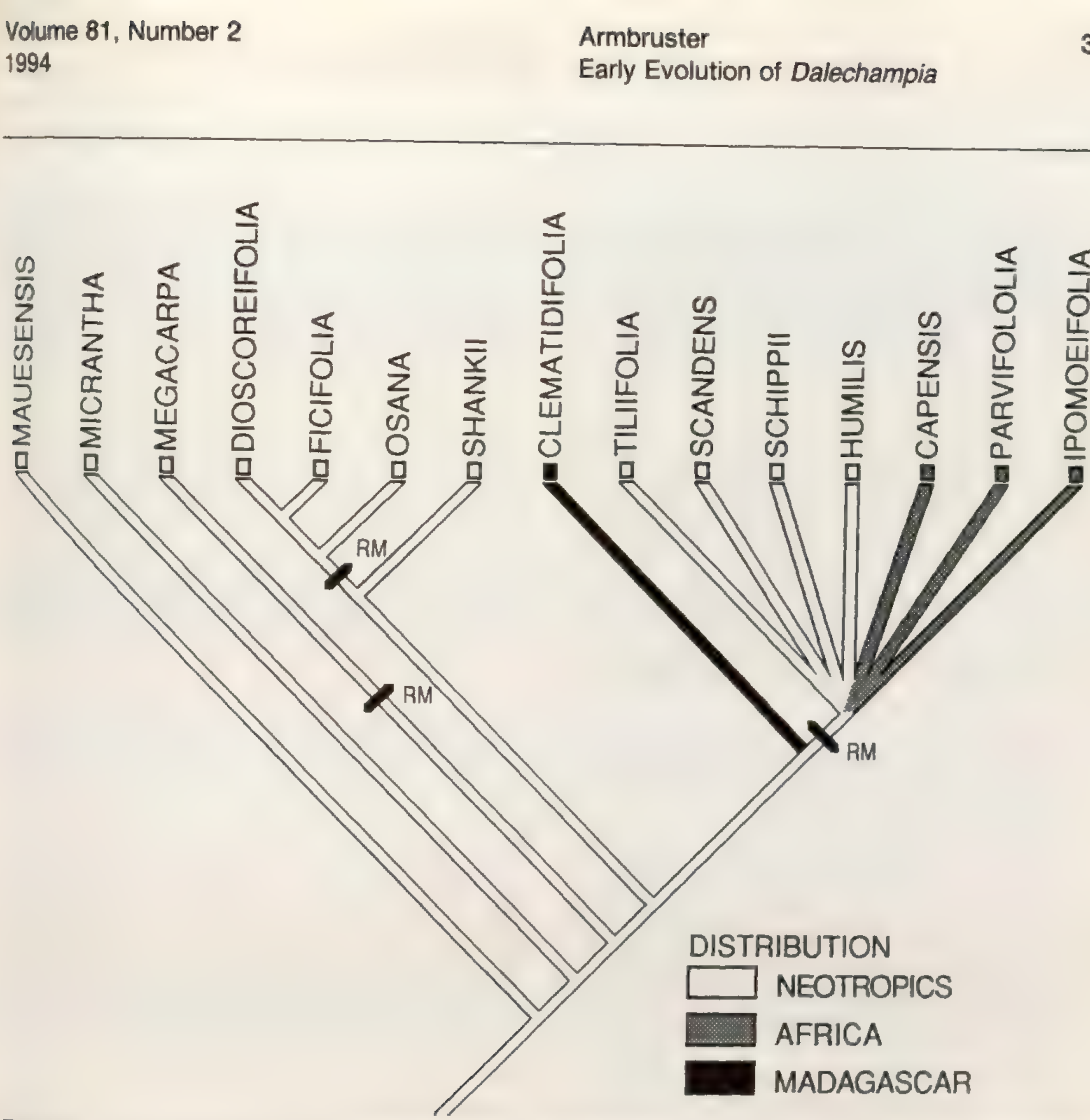

FIGURE 6. Consensus tree for the simplified set of taxa, assuming that all characters are reversible except character 17 (see Table 2), which was assumed irreversible. The figure shows the species distribution mapped onto the cladogram and origins of the mutualism with resin-collecting bees ("resin mutualism" = RM). Taxa with unstable arrangements in the 252 maximally parsimonious trees are indicated by polytomies.

did with lepidopteran symbionts), and it colonized the Old World by some mode other than long-distance dispersal, we might expect to see sister genera of bees visiting *Dalechampia* on either side of the Atlantic as we observed in the lepidoptera. We do not see this; there are not close phylogenetic relationships between the major pollinators in the New World and the Old. The most likely candidates, *Hypanthidium* on neotropical *Dalechampia* and *Pachyanthidium* on South African *Dalechampia* (Steiner & Whitehead, 1990; Armbruster & Steiner, 1992), are not particularly close within the Anthidiini (C. D. Michener, pers. comm.). This suggests dispersal between continents either was long-distance over oceanic barriers to bees, or occurred prior to the evolution of the resin mutualism (consistent with H_3 but not H_1), or somehow occurred without the bees "following" the plant.

A somewhat surprising feature of H_1 is that it has the *Dalechampia* that colonized Madagascar abandoning pollination by resin-collecting bees and reverting to pollination by pollen-collecting bees and beetles. This is surprising because pollination by resin-collecting bees appears to be a very successful pollination system, as evidenced by its abundance in the genus (some 80% of *Dalechampia* species are pollinated in this way). If this occurred, we could expect there to be some disadvantage to pollination by resin-collecting bees in Madagascar. There might actually be such a disadvantage; according to C. D. Michener (pers. comm.), except for tiny *Trigona* spp., which are often too small to be effective pollinators (see Armbruster & Mziray, 1987; Armbruster, 1988), resin-collecting bees are notably uncommon in Madagascar.

Discussion and Conclusions

In this study I have tried to illustrate the advantages of using the results of cladistic analyses to develop and refine hypotheses about the bio-

geographic and evolutionary history of extant organisms for which there are no detailed fossil records. However, many uncertainties remain, and it is essential to explore through iterative analysis the consequences of making different assumptions about character evolution. The use of molecular data to infer phylogeny may solve some of the problems and uncertainties illustrated here, but even molecular phylogenies often may be ambiguous (see Sanderson & Donoghue, 1989). Tests of phylogenetic and historical hypotheses using independent data (such as information on symbionts) are necessary if we are to progress beyond the stage of hypothesis generation.

In the present study, I used cladistic results to generate and refine several hypotheses explaining the present distribution of *Dalechampia* species and their pollination systems. Three competing hypotheses seem most likely, and independent data are needed to distinguish among these. In particular, information on the genetics and development of flowers and inflorescences would be valuable, because the phylogenetic and biogeographical inferences made were sensitive to assumptions about the reversibility to the primitive character states of certain inflorescence characters.

Independent ecological information was used to evaluate the likelihood of the hypotheses generated from phylogenetic information. Data from insect herbivores and pollination of *Dalechampia* best support Hypothesis 3. The evidence, however, does not exclude Hypotheses 1 or 2. Hypothesis 1 depends on the assumption that all morphological characters can revert to their primitive stages. Whether this is realistic remains to be determined.

It appears that *Dalechampia* originated in the Neotropics or western Gondwana. The earliest species of *Dalechampia* probably employed fragrance-collecting male euglossine bees or pollen-collecting insects as pollinators. The mutualism with resin-collecting bees may have evolved separately in the Old and New Worlds (Hypothesis 3), or may have evolved only in the New World (Hypotheses 1 and 2).

The simplest biogeographic scenario is proposed in Hypothesis 1: *Dalechampia* originated in the New World, evolved a mutualism with resin-collecting bees there, and subsequently colonized Africa and Asia, and most recently, Madagascar, where the mutualism with resin-collecting bees was lost. This explanation is similar to explanations of the dispersal history of a number of plant groups (Raven & Axelrod, 1974). For example, the usual explanation of pantropical distribution of the Malpighiaceae is that the group originated in South America in the late Cretaceous/early Tertiary, evolved a mutualism with oil-collecting bees (based on oil secretion by calyx glands), and more recently colonized the Paleotropics, where the mutualism was lost (Raven & Axelrod, 1974; Anderson, 1979).

A recent re-evaluation of floral morphology of Malpighiaceae by Vogel (1990) leads to an alternative conclusion: the Malpighiaceae originated in western Gondwana in the mid-Cretaceous, and continental drift resulted in primitively glandless species occurring in both the Paleotropics and Neotropics. One (or several?) lineage(s) in the Neotropics evolved a mutualism with oil-collecting bees, and, later, members of this advanced lineage recolonized the Paleotropics (Vogel, 1990). This scenario is similar to Hypotheses 2 and 3 for *Dalechampia*: the presence of species with predominately plesiomorphic character states in the Old and New Worlds is explained by a widespread, possibly Gondwanan distribution of *Dalechampia* during the mid-Cretaceous to early Tertiary. The close similarity of some of the derived species of the Old and New Worlds is explained by a second trans-Atlantic dispersal event in both Malpighiaceae and *Dalechampia*. It will be interesting to see if additional evidence continues to support these earlier origins and more complex biogeographic scenarios for *Dalechampia*, Malpighiaceae, and possibly other plant groups.

Literature Cited

Ackery, P. R. 1988. Hostplants and classification: A review of nymphalid butterflies. Biol. J. Linn. Soc. 33: 95–203.

Anderson, W. R. 1979. Floral conservatism in neotropical Malpighiaceae. Biotropica 11: 219–223.

Armbruster, W. S. 1983. *Dalechampia scandens*. Pp. 230–233 *in* D. H. Janzen (editor), Costa Rican Natural History. Univ. Chicago Press, Chicago, Illinois.

———. 1984. The role of resin in angiosperm pollination: Ecological and chemical considerations. Amer. J. Bot. 71: 1149–1160.

———. 1988. Multilevel comparative analysis of morphology, function, and evolution of *Dalechampia* blossoms. Ecology 69: 1746–1761.

——— & W. Mziray. 1987. Pollination and herbivore ecology of an African *Dalechampia* (Euphorbiaceae): Comparisons with New World species. Biotropica 19: 64–73.

——— & K. E. Steiner. 1992. Pollination ecology of four *Dalechampia* species (Euphorbiaceae) in northern Natal, South Africa. Amer. J. Bot. 79: 306–313.

——— & G. L. Webster. 1979. Pollination of two species of *Dalechampia* (Euphorbiaceae) in Mexico by euglossine bees. Biotropica 11: 278–283.

———, A. L. Herzig & T. P. Clausen. 1992. Pol-

lination of two sympatric species of *Dalechampia* (Euphorbiaceae) in Suriname by male euglossine bees. Amer. J. Bot. 79: 1374–1381.

———, S. Keller, M. Matsuki & T. P. Clausen. 1989. Pollination of *Dalechampia magnoliifolia* (Euphorbiaceae) by male euglossine bees (Apidae: Euglossini). Amer. J. Bot. 76: 1279–1285.

———, M. E. Edwards, J. F. Hines, R. L. A. Mahunnah & P. Munyenyembe. 1993. Evolution and pollination of Madagascan and African *Dalechampia*. Research and Exploration 9: 430–444.

Cammerloher, H. 1931. Blüten Biologie I. Gebrüder Borntraeger, Berlin.

DeVries, P. J. 1987. The Butterflies of Costa Rica and Their Natural History. Princeton Univ. Press, Princeton, New Jersey.

Donoghue, M. J. 1989. Phylogenies and the analysis of evolutionary sequences, with examples from seed plants. Evolution 43: 1137–1156.

Dressler, R. L. 1982. Biology of the orchid bees (Euglossini). Annual Rev. Ecol. Syst. 13: 73 94.

Humphries, C. J. & L. R. Parenti. 1986. Cladistic Biogeography. Clarendon, Oxford.

Maddison, W. P. & D. R. Maddison. 1992. MacClade. Sinauer, Sunderland, Massachusetts.

———, M. J. Donoghue & D. R. Maddison. 1984. Outgroup analysis and parsimony. Syst. Zool. 33: 83–103.

Magin, N. 1987. The pseudanthium of *Dalechampia* and its systematic significance. XIV International Botanical Congress, Berlin. [Abstract.]

Michaelis, P. 1924. Blutenmorphologische Untersuchungen an den Euphorbiaceen. Bot. Abh. 3: 1-150.

Michener, C. D. 1979. Biogeography of the bees. Ann. Missouri Bot. Gard. 66: 277–347.

Otero, L. D. 1990. Estudio de algunas caracteres para su uso en la clasificación de Eurytelinae (Lepidoptera: Nymphalidae). Bol. Entomol. Venez. 5: 123–138.

Raven, P. H. & D. I. Axelrod. 1974. Angiosperm biogeography and past continental movements. Ann. Missouri Bot. Gard. 61: 539–673.

Sanderson, M. J. & M. J. Donoghue. 1989. Patterns of variation in levels of homoplasy. Evolution 43: 1781–1795.

Steiner, K. E. & V. B. Whitehead. 1991. Resin collection and the pollination of *Dalechampia capensis* (Euphorbiaceae) by *Pachyanthidium* (Megachilidae) in South Africa. J. Entomol. Soc. South Africa 54: 67–72.

Swofford, D. 1993. PAUP. Phylogenetic Analysis Using Parsimony, version 3.0. Illinois Natural History Survey, Champaign, Illinois.

Vogel, S. 1990. History of the Malpighiaceae in the light of pollination ecology. Mem. New York Bot. Gard. 55: 130–142.

Webster, G. L. 1975. Conspectus of a new classification of the Euphorbiaceae. Taxon 24: 593 601.

———. 1994. Synopsis of the suprageneric taxa of Euphorbiaceae. Ann. Missouri Bot. Gard. 81: 33-144.

——— & W. S. Armbruster. 1991. A synopsis of the neotropical species of *Dalechampia* (Euphorbiaceae). Bot. J. Linn. Soc. London 105: 137–177.

——— & B. D. Webster. 1972. The morphology and relationships of *Dalechampia scandens* (Euphorbiaceae). Amer. J. Bot. 59: 573–586.

Whitten, W. M., A. M. Young & N. H. Williams. 1989. Function of glandular secretions in fragrance collection by male euglossine bees (Apidae: Euglossini). J. Chem. Ecol. 15: 1285–1295.

Appendix. List of specimens studied.

D. aristolochiifolia HBK: Armbruster et al. 87-128, 87-136 (ALA); Chavez 3067 (MO); Cook & Gilbert 1022 (F); Dillon & Turner 1703 (F, MO); Gentry et al. 44120, Hudson 1192, Hutchison & Wright 3852 (MO); MacBride 3802 (F); Sagastegui et al. 8455, Stein & Todzia 2064 (MO); Stork & Horton 10093, Stork et al. 10563 (F); Vargas 131, Woytkowski 5720, 6564, 6834 (MO). *D. attenuistylus* Armbruster: Armbruster et al. 87-153, Armbruster 93-01 (ALA).

D. canescens HBK: Armbruster & Herzig 85-119, 85-127 (ALA); Haught 1832, Plowman & Vaughan 5354 (F); Webster & Armbruster 23651 (ALA). *D. capensis* Spreng.: Armbruster & Steiner 90-202, Armbruster et al. 90-203 (ALA); Bayliss 5294, Coetzee 1328, Dahlstrand 1952, Germishuizen 233, Huntley 79, Kemp 760, Kerfoot K7301, Strey 11185, Zeyher 245 (MO). *D. caperonioides* Baill.: Webster et al. 25245 (ALA). *D. chlorocephala* M. Denis: Armbruster et al. 90-151; Dorr & Koenders 2987, 2987A, 3024 (ALA, MO). *D. clematidifolia* Baill.: Armbruster et al. 90-148 (ALA); Croat 29424, 30130, 31463, 32153 (MO).

D. dioscoreifolia Poepp.: Armbruster 79-212, Armbruster et al. 85-117, 87-139 (ALA); Beekman 59, Feuillet 417 (CAY); Gentry 6365 (ALA, MO); Gentry et al. 18696 (MO); Granville et al. 7292 (B, CAY, MO, P); Guanchez & Huber 4742 (ALA, VEN); Maas et al. 2226 (CAY, U); Oldeman 2067 (CAY, MO, NY, P); Oldeman B.3227 (CAY, NY, U); Poncy 89 (ALA); Proctor et al. 27384 (F); Raynal-Roques 20006 (CAY); Revilla 1710 (MO).

D. ficifolia Lam.: Hatschbach 44381 (F); Webster et al. 25007, Webster & Armbruster 25101, 25161 (ALA). *D. fragrans* Armbruster: Armbruster & Herzig 85-101 (ALA, NY); Armbruster & Herzig 85-104 (ALA); Maas et al. 2320 (MO); Mori et al. 8693 (NY, P).

D. heteromorpha Pax & Hoffm.: Armbruster 77302, 77306, 77405, 78414, 78422, 79-201, 79-210, 79-217, Armbruster et al. 87-119, 87-134, 87-135 (ALA); Foster 11920 (ALA, F); Webster & Armbruster 22073 (ALA). *D. humilis* Muell. Arg.: Webster et al. 25275 (ALA).

D. ipomoeifolia Benth.: Ash 2422, Dalziel 1270, de Wilde 5955, 6872, Grant 4024, Harris 1784, Katende & Lye K440, Westphal & Westphal-Stevens 3497 (MO).

D. kirkii Prain: Lavranos 4915, Story 1663 (MO).

D. liesneri Huft: Armbruster et al. 87-142, 87-143 (ALA). *D. luetzelburgii* Pax & Hoffm.: Luetzelburg 132 (MO).

D. "mauesensis" sp. nov.: Murça Pirez 50 (VEN). *D. megacarpa* Armbruster: Armbruster et al. 85-115, 87-151 (ALA). *D. micrantha* Poepp.: Armbruster et al. 85-113, 87-150, 87-156 (ALA); Byron & Coelho 443 (MO); Garcia-Barriga 14103 (NY); Gentry et al. 29955 (F); Lindeman et al. 214 (U); MacRae & Ruiz 80 (F); Nee 31877 (MO); Poeppig 2807 (P); Poeppig 7200 (MO); Prance et al. 24587 (NY); Revilla 87 (F, MO, NY); Rimachi 323 (NY); Schomburgk 783 (P); Spichiger & Encarnacion 1014 (MO, NY); Spichiger & Encarnacion 1037 (MO); Vasquez et al. 666 (F, MO, NY); Wessels Boer 454 (K, NY, U); Williams 3629 (US).

D. osana Armbruster: Burger & Liesner 7278, Burger & Gentry 8962, 9011 B, Gomez 19672, Liesner 1869, Utley & Utley 1214 (F).

D. parvibracteata Lanj.: Jenman 4088 (US); McDowell & Gopaul 2264 (ALA, US). *D. parvifolia* Lam.: Armbruster et al. 90-168, Armbruster & Steiner 90-195 (ALA). *D. pentaphylla* Lam.: Hatschbach 11840, Mexia 4149, Regnelli 1051 (F); Webster et al. 25215 (ALA); Woytkowski 35147 (F).

D. scandens L.: Alexandre 227 (CAY); Armbruster & Herzig 85-107, 85-124, Armbruster et al. 87-103, 87-107, 87-115, 87-140 (ALA); Benoist 835, 1262 (P); Billiet & Jadin 4332 (BM, CAY); Broadway 444 (US); Cremers & Hoff 10608, Feuillet 538, 2969 (CAY); Gentry & Revilla 16246, Gentry et al. 22702 (MO); Gillespie & Persaud 1046, Gillespie et al. 1654, 1655, 1781 (ALA, US); Granville 6940 (B, CAY, P); Harrison 714 (K); Harrison 1769 (K, NY); Hekking 1049 (U); Hitchcock 16770, Irwin BG-71 (US); Irwin et al. 55831 (MO, NY, U, US); Kappler 1888 (P, U); Lall 312 (U); Lanjouw & Lindeman 1114, 1807 (NY, U); L.B.B. (J.T. Serringa) 12534 (U); Maas et al. 7222 (B, US); Prevost 1456 (CAY); Reitsma & Reitsma 852 (NY); Sagot 512 (BM, P); Schomburgk 610 (BM); Service Forestier 3077 (U); Service Forestier 4328 (CAY, P, U); Skog et al. 7427 (CAY, NY, P, U, US); Solomon 8899 (MO); Solomon & Escobar 12486 (ALA, MO); Wachenheim 25 (P); Webster 24143 (NY, U); Webster & Armbruster 23508, 23523, 25105 (ALA). *D. schippii* Standley: Armbruster 77-303, 78-416, 79-204 (ALA). *D. schottii* Greenm.: Armbruster 77-305, 78-409 (ALA). *D. shankii* (Molina) Huft: Armbruster 79-213, 91-102, Armbruster & Berg 85-128 (ALA); Cuatrecasas 21512, Davidson 6828, Shank & Molina 4427, 4475, Standley & Valerio 48588 (F). *D. spathulata* Baill.: Croat 20306, Poeppig 2380, Vigo 6480, 7693 (MO); Williams 4189 (F). *D. subternata* Muell. Arg.: Armbruster et al. 90-144, 90-150, Armbruster & Hines 90-158, 90-160, 90-162, 90-164 (ALA); Croat 30708, 30744, 31022, 31065, Dorr 3050, Gentry 11801 (MO); Gillespie 4180, 4181 (ALA, US); Lorence 2097 (MO); Miller & Keating 4527, Phillipson 2492, 3050 (ALA, MO).

D. tiliifolia Lam.: Armbruster et al. 85-108, 85-111, 87-111, 87-125, 87-138, 87-141 (ALA); Barthelemy 145 (CAY); Broadway 631 (NY); Cremers 9429 (B, CAY, MO, NY, P, US); Feuillet 1754 (CAY, P); Forest Dept. Brit. Guy. 5978 (K, NY); Granville 260 (CAY, P, U); Granville 265 (CAY); Hoff 5357 (B, CAY, NY, P, US); Mori et al. 15026 (CAY, P); Oldeman B-802 (CAY, U); Picon et al. 1524 (ALA, VEN); Poncy 4 (P); Prevost 1808 (CAY, U, US); Sagot 513 (P); Solomon 3248, 7586 (MO); Webster & Armbruster 23712 (ALA). *D. triphylla* Lam.: Armbruster & Herzig 85-103 (ALA); Barreto 5058, Henschen 1052 (F); Webster & Armbruster 25182, 25189, 25218 (ALA).

Plukenetia spp.: Armbruster 78-420, Armbruster et al. 85-106, 87-110, 87-113, 87-144, Webster & Armbruster 23412 (ALA).

Tragia spp.: Armbruster et al. 90-146, Armbruster & Hines 90-157, 90-159, 90-163 (ALA); Maas 6231 (MO).

POLLEN MORPHOLOGY AND PHYLOGENY OF THE TRIBE PLUKENETIEAE (EUPHORBIACEAE)[1]

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ABSTRACT

A scanning electron microscopy and light microscopy survey of pollen morphology in the Plukenetieae (Euphorbiaceae) was undertaken to help elucidate phylogenetic relationships within the tribe. Pollen is medium to large, spheroidal to suboblate, and tricolpate, inaperturate, or with poorly defined apertures. Subtribe Plukenetiinae is characterized by tricolpate pollen with uneven-margined colpi and a perforate to reticulate tectum. Pollen evidence supports a division between genera having an aborescent habit (*Angostyles*, *Astrococcus*, and *Haematostemon*) and those with a scandent habit (*Plukenetia* and *Romanoa*). The synonymy of the monotypic genera *Vigia* and *Eleutherostigma* with *Plukenetia* is also supported. Subtribe Tragiinae is exceptionally diverse in pollen morphology. Aperture condition ranges from tricolpate, the plesiomorphic and most common state, to weakly aperturate and inaperturate; islands, fragments, or strands of sexine are usually present on the apertural membrane, and aperture margins are uneven and often indistinct. Exine sculpture is punctate, foveolate, reticulate, rugulate, or baculate. The large genus *Tragia* includes seven distinct pollen types, with most sections (e.g., *Bia*, *Ctenomeria*, *Leptobotrys*, *Tragia*, and *Zuckertia*, and also subgenus *Mauroya*) characterized by a uniform and unique pollen morphology, supporting the sectional classification of *Tragia*. The other Tragiinae genera have pollen distinct from *Tragia*, with the exception of *Tragiella*, which closely resembles sections *Tagira* and *Lassia*. Pollen evidence supports *Cnesmone* and *Megistostigma* as sister taxa, and suggests a close relationship with *Pachystylidium*. *Acidoton* includes two different pollen types; the inaperturate type closely resembles pollen of *Platygyna*, suggesting that *Acidoton* may not be monophyletic and the tricolpate species perhaps represents a distinct genus. Pollen, together with floral morphological evidence, supports the hypothesis of section *Zuckertia* as a plesiomorphic member of *Tragia*, and suggests that *Tragia* is paraphyletic and that the smaller Tragiinae genera are derived from *Tragia*.

The Plukenetieae belong to the Acalyphoideae, the largest and least understood of the five euphorbiaceous subfamilies. The tribe includes 13 genera distributed worldwide in tropical and warm temperate regions. Many species are twining vines or lianas, both unusual habits in the family; other species are erect herbs, shrubs, or rarely small trees. Although flowers are small and apetalous, floral morphology is diverse, particularly the style and androecium. Another uncommon feature is the presence of stinging hairs in many species. *Tragia* L. is the largest genus, with more than 125 species, some of which are commonly known as nose burns. All other genera have fewer than 17 species each; many are monotypic or with few species. Circumscription of genera and infratribal phylogenetic relationships are the principal systematic problems in the Plukenetieae.

Pollen morphology has been invaluable in the systematics of the Euphorbiaceae (Punt, 1962; Köhler, 1965). Light microscopic (LM) observations by Punt (1962), in his pollen survey of the Euphorbiaceae, revealed a diversity of pollen types among species belonging to the Plukenetieae. The present study of pollen morphology of the Plukenetieae based on scanning electron microscopy (SEM) and LM was initiated to help resolve problems of generic circumscription and elucidate phylogenetic relationships. The study is the first part of a larger project concerning the evolutionary

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history of the Plukenetieae, which will include cladistic analyses based on floral, vegetative, and other characters, studies of trends in character evolution, and an attempt at correlating the unusual and often bizarre diversity in floral morphology with pollination biology. Determining plesiomorphic character states and the direction of evolutionary trends will also be of importance in phylogenetic studies of other genera for which the Plukenetieae or its members have been considered as outgroup(s), such as *Dalechampia* L. (Armbruster, 1994) and *Omphalea* L. (Gillespie, 1988).

There have been many additions and taxonomic changes in the Plukenetieae since it was first recognized as a distinct group by Bentham (1880, as subtribe "Plukenetieae"). The circumscription of the tribe and its genera recognized closely follows that of Webster (1975, 1994) in his classification of the Euphorbiaceae. Two exceptions are recognition of the genera *Tragiella* Pax & K. Hoffm. (following Radcliffe-Smith, 1982, 1987) and *Pachystylidium* Pax & K. Hoffm. (following Airy Shaw, 1969, 1975), both originally described as species of *Tragia*. In addition, several taxonomic and nomenclatural changes have taken place since Webster's 1975 synopsis. The monotypic genera *Vigia* Vellozo (which has priority over the more commonly used generic name *Fragariopsis* A. St. Hil.) and *Eleutherostigma* Pax & K. Hoffm. have been synonymized under *Plukenetia* (Gillespie, 1993). Adrien Jussieu's genus *Anabaena* has been twice renamed, as *Romanoa* by Trevisan (1848) and as *Anabaenella* by Pax & Hoffmann (1919), due to similarity with its namesake cyanobacteria. Although the cyanobacteria were originally described as *Anabaina* Bory, the more commonly used name of *Anabaena* Bory was recently conserved against *Anabaena* Adr. Juss. (ICBN, Greuter, 1988: 112). *Romanoa*, the name rediscovered by Punt (1962) and Radcliffe-Smith (1980), thus becomes the valid name for the genus.

The most recent monograph of the Plukenetieae (as subtribe Plukenetiinae of tribe Acalypheae) was by Pax & Hoffmann (1919; with additions and changes, 1924, 1931). The authors treated a number of segregate genera in addition to *Tragiella* and *Pachystylidium* that were not recognized by Webster (1975); these are *Gitara* Pax & K. Hoffm., considered synonymous with *Acidoton* Sw. (Webster, 1967), and *Tetracarpidium* Pax (also known as *Angostylidium* (Muell. Arg.) Pax & K. Hoffm.), *Apodandra* Pax & K. Hoffm. and *Pterococcus* Hassk., all presently treated under *Plukenetia* L. (Gillespie, 1993). A second difference is Webster's recognition of *Megistostigma* Hook. f. following Croizat (1941) and Airy Shaw (1969); of the two species treated by Pax and Hoffmann, *M. malaccense* Hook. f. was considered a species of *Sphaerostylis* Baill. and *M. peltatum* (J. J. Sm.) Croizat as the monotypic *Clavistylus* J. J. Sm. The genus *Ramelia* Baill. has since been reduced to synonymy under *Bocquillonia* Baill. (Acalyphoideae, tribe Alchornieae) and thus excluded from the Plukenetieae (Airy Shaw, 1968, 1974), while *Megalostylis* is now considered to be a synonym of *Dalechampia* (Webster & Armbruster, 1991).

In his most recent classification, Webster (1994) treats *Dalechampia* as a subtribe, the Dalechampiinae, of the Plukenetieae, rather than as a distinct but related tribe (as in Webster, 1975). Although the genus will not be extensively treated in the present paper, its pollen morphology will be discussed in relation to the Plukenetieae.

In the first attempt at an infratribal classification and consideration of relationships, Pax & Hoffmann (1919) divided the 19 genera of their "Plukenetiinae" into four informal groups, Plukenetiiformes, Astrococciformes, Tragiiformes, and Sphaerostyliformes, based primarily on stamen number and style shape. Webster (1975) created the first formal subtribal classification upon describing the Tragiinae. The Tragiinae are characterized by presence of stinging hairs, a trilocular ovary, and absence of foliar glands; species are found in all habitats but are particularly diverse in dry areas. In contrast, the Plukenetiinae are characterized by absence of stinging hairs, foliar glands typically present and an ovary that is usually 4-locular or less often trilocular, and are usually found in wet habitats. Style morphology has been used extensively in infratribal classification and generic delimitation. With the exception of the genus *Tragia*, there has been an unusual radiation in style morphology in the Plukenetieae. Within subtribe Tragiinae, many of the genera are characterized and differentiated from *Tragia* on the basis of unusually shaped massive styles (e.g., *Sphaerostylis*, *Megistostigma*, *Cnesmone* Blume, and *Tragiella*). Pax & Hoffmann (1919, 1931) based their sectional classification of *Plukenetia* on style morphology.

Since *Tragia* is a large and diverse genus it is necessary to consider an infrageneric classification. Eight sections are recognized in the present study. The sectional classification of Pax & Hoffmann (1919, 1931) is followed with the following exceptions. Section *Leptobotrys* (Baill.) Muell. Arg. is considered distinct from section *Tragia*, whereas sections *Leucandra* (Klotzsch) Muell. Arg. and *Ratiga* Muell. Arg. are treated as part of section

Tragia (following Miller & Webster, 1967, and Múlgura de Romero & Gutiérrez de Sanguinetti, 1989). Also considered is Léandri's subgenus *Mauroya*, which includes a single Madagascan species. Many of the sections have in the past been recognized as distinct genera (e.g., *Bia* Klotzsch, *Ctenomeria* Harv., *Lassia* Baill., *Leptobotrys* Baill., *Leucandra* Klotzsch, and *Zuckertia* Baill.).

Previous pollen morphological studies of the Plukenetieae have been based only on LM (Erdtman, 1952; Punt, 1962; Miller & Webster, 1967), with the exception of studies dealing only briefly with pollen morphology (e.g., Gillespie, 1988; Múlgura de Romero & Gutiérrez de Sanguinetti, 1989). The most extensive survey was that of Punt (1962), who examined 17 genera (equivalent to 12 in the classification followed here) in his pollen survey of the Euphorbiaceae. Pollen types within the tribe fell into two of Punt's 17 main groups, the *Plukenetia* configuration and the *Cnesmosa* (= *Cnesmone*) configuration. The *Plukenetia* configuration is characterized by oblate-spheroidal to oblate, tricolpate or triporate grains with broad apertures having a "ruptured membrane." Of the two types within this main group, the *Plukenetia* type is tricolpate and includes all examined species of the Plukenetiinae, African Tragiinae, and most New World *Tragia* spp. The *Pachystylidium* type is triporate and includes only that genus. The *Cnesmosa* configuration is characterized as inaperturate and lacking a crotonoid exine; three of its five types are composed of species of the Plukenetieae. The *Cnesmosa* type of pollen with a psilate exine includes *Acidoton*, *Megistostigma*, and *Cnesmone*. The *Tragia fallax* type of pollen is described as having an "intectate pilate exine" and consists of *Tragia* sect. *Bia* (Klotzsch) Muell. Arg. The *Platygyne* (= *Platygyna*) type of pollen with an exine that is tectate and "intra-reticulate" (defined by Punt as "columellae inside the tectum form[ing] a network") consists only of species of *Platygyna* Mercier Punt concluded that pollen morphology supported the distinctness of *Tragia* sect. *Bia*, the close relationship of *Haematostemon* (Muell. Arg.) Pax & K. Hoffm., *Angostyles* Benth., and *Astrococcus* Benth., and the observation that *Apodandra*, *Romanoa*, *Fragariopsis* (= *Vigia*), *Pterococcus*, and *Angostylidium* cannot be easily distinguished from *Plukenetia*. Pollen evidence also supported Croizat's (1941) circumscription of *Sphaerostylis* and *Megistostigma*. Miller & Webster (1967) examined pollen of *Tragia* species from the United States; evidence from their study of pollen and floral morphology led them to revive section *Leptobotrys* (Baill.) Muell. Arg., which was considered part of section *Tragia* by Pax & Hoffmann (1919), and to doubt the taxonomic validity of section *Leucandra* (Klotzsch) Muell. Arg.

Methods

Flowers were removed from herbarium specimens, of which determinations were verified, and rehydrated in 3% Aerosol-OT for 3–4 days. Pollen grains were isolated and mounted in Hoyer's medium (Radford et al., 1974) for examination under LM. The method of Lynch & Webster (1975) was followed for SEM studies. Pollen grains were dehydrated to 100% ethanol, to 100% amyl acetate, and then critical-point dried. Following sputter coating with gold or a gold/palladium mixture, grains were examined and photographed in an ISI DS130 (equipped with a LaB_6 filament), Hitachi S800, or Cambridge 250 scanning electron microscope. All pollen was prepared in the above manner unless specified otherwise. In several cases pollen was acetolyzed (following the method of Erdtman, 1952) then mounted directly on a stub and sputter coated for examination under SEM. Voucher microscope slides and electron micrographs are deposited at the Systematics Laboratory, Botany Department, University of California, Davis. Voucher LM slides of acetolyzed pollen are deposited at the Palynology Laboratory, Botany Department, Smithsonian Institution, Washington, D.C.

Descriptions of pollen grains are based on observations under LM and SEM. Measurements were made under LM on 15 grains mounted in Hoyer's medium. The polar axis (P), equatorial axis (E), and the polar to equatorial axis ratio (P/E) are given in the generic descriptions as the range of mean values of collections examined (refer to Table 1 for measurements of individual collections). In the case of inaperturate grains that are ellipsoidal in shape, the shortest axis (S) and longest axis (L) are given. Exine thickness of aperturate grains was measured at mid mesocolpium in polar view. Terminology used follows that of Erdtman (1952, 1966) and Walker & Doyle (1975). In the present paper the term scabrate is restricted to the description of a surface having a covering of microprojections that are irregular in size, shape, and distribution (e.g., Figs. 27, 48, 69). The term microverrucae (e.g., Figs. 9, 38, 41, 43) is introduced to refer to microprojections that are more regular in size, wider than high, and rounded in shape but not constricted at the base (as distinguished from conical spinules and constricted-based microgemmae).

Twelve of the 13 genera in the Plukenetieae

TABLE 1. Species of Plukenetieae examined with voucher information, geographical location, pollen size dimensions (minimum–maximum (mean)) of polar axis (P Axis) and equatorial axis (E Axis), all in μm, and pollen shape given as ratio of polar to equatorial axes (P/E). Inaperturate pollen is indicated by an asterisk; shortest axis (under P Axis) and longest axis (under E Axis) are given if pollen shape is ellipsoid, otherwise a single diameter is given if spheroidal. Pollen with apertures not easily visible under LM is indicated by a "c"; shortest and longest axes are given. Measurements of acetolyzed pollen are preceded by an "a."

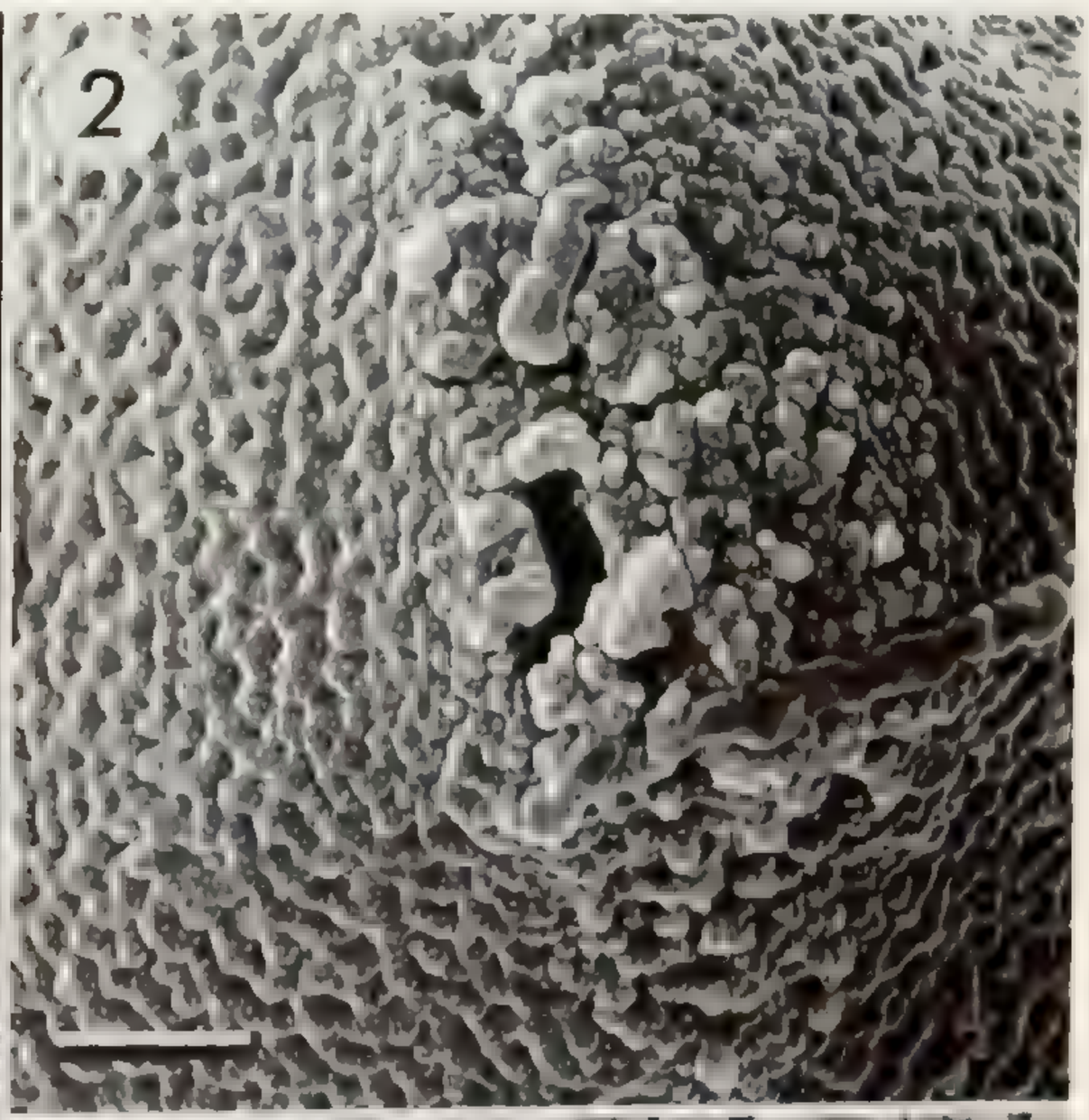
Species	Collection	Location		P Axis	E Axis	P/E
Plukenetiinae						
Angostyles longifolia Benth.	*Spruce 2282*, NY	Brazil		52–60 (54)	58.5–67.5 (62)	0.87
Astrococcus cornutus Benth.	*Liesner 8693*, NY	Venezuela		43.5–52 (48)	50.5–57.5 (54.5)	0.88
A. cornutus Benth.	*Liesner 8693*, NY	Venezuela	a	34.5–41.5 (37.5)	41.5 48.5 (46)	0.82
Eleutherostigma lehmannianum Pax & K. Hoffm.	*Cazalet & Pennington 5089*, UC	Ecuador		48.3–53 (50.5)	53 -60 (56.5)	0.89
Haematostemon coriaceus (Baill.) Pax & K. Hoffm.	*Wurdack & Adderley 43210*, NY	Venezuela		33.5–37 (35)	38–43.5 (40.5)	0.86
H. guianensis Sandw.	*Fanshawe 2869*, US	Guyana		41.5–46 (44)	47–50.5 (49.5)	0.89
Plukenetia africana Sond.	*Pope et al. 834*, MO	Botswana		34–39 (36.5)	43–49.5 (45.5)	0.80
P. africana Sond.	*Wild 5062*, MO	Botswana		34–40.5 (36.5)	40.5–48 (44)	0.83
P. brachybotrya Muell. Arg.	*Vargas 18799*, US	Peru		49.5–57 (53)	60–67.5 (62)	0.85
P. conophora Muell. Arg.	*Zenker 3394*, US	Cameroon		34–37.5 (35)	41.5–45.5 (42.5)	0.82
P. conophora Muell. Arg.	*Zenker 3394*, US	Cameroon	a	27.7–32 (30.5)	32–41.5 (36.5)	0.84
P. corniculata Smith	*Koorders 41720*, UC	Indonesia		34.5–37 (35)	41.5–46 (43.5)	0.80
P. loretensis Ule	*Fosberg 29094*, MO	Peru		50.5–62 (55)	60–76 (66.5)	0.83
P. loretensis Ule	*Maguire & Politi 27371*, US	Venezuela		48.5–57.5 (53)	57.5–69 (64)	0.83
P. penninervia Muell. Arg.	*Werff & Wingfield 3173*, DAV	Venezuela		30–39 (34)	39–48 (43)	0.79
P. penninervia Muell. Arg.	*Standley 56708*, A	Honduras		35–43 (37.5)	45.5–52 (48)	0.79
P. polyadenia Muell. Arg.	*Lindeman 6134*, DAV	Surinam		50.5–60 (56)	57.5–69 (63)	0.89
P. madagascariensis Léandri	*Morat 4893*, P	Madagascar		37.5–40.5 (39)	43–46 (45.5)	0.86
P. multiglandulosa Jabl.	*Cowan & Wurdack 31400*, US	Venezuela		32.5–37.5 (35)	40.5–47 (43.5)	0.80
P. stipellata L. J. Gillespie	*Gillespie 418*, DAV	Costa Rica		53–60 (56)	57.5–69 (64.5)	0.87
P. supraglandulosa L. J. Gillespie	*Cowan 38204*, US	French Guiana		31–33 (32)	39–45 (41)	0.78
P. verrucosa Smith	*Prance et al. 11255*, DAV	Brazil		34.5–39 (37)	42.5–50.5 (46.5)	0.80
P. volubilis L.	*Asplund 14129*, US	Peru		49.5–58.5 (53)	58.5–65 (62)	0.85

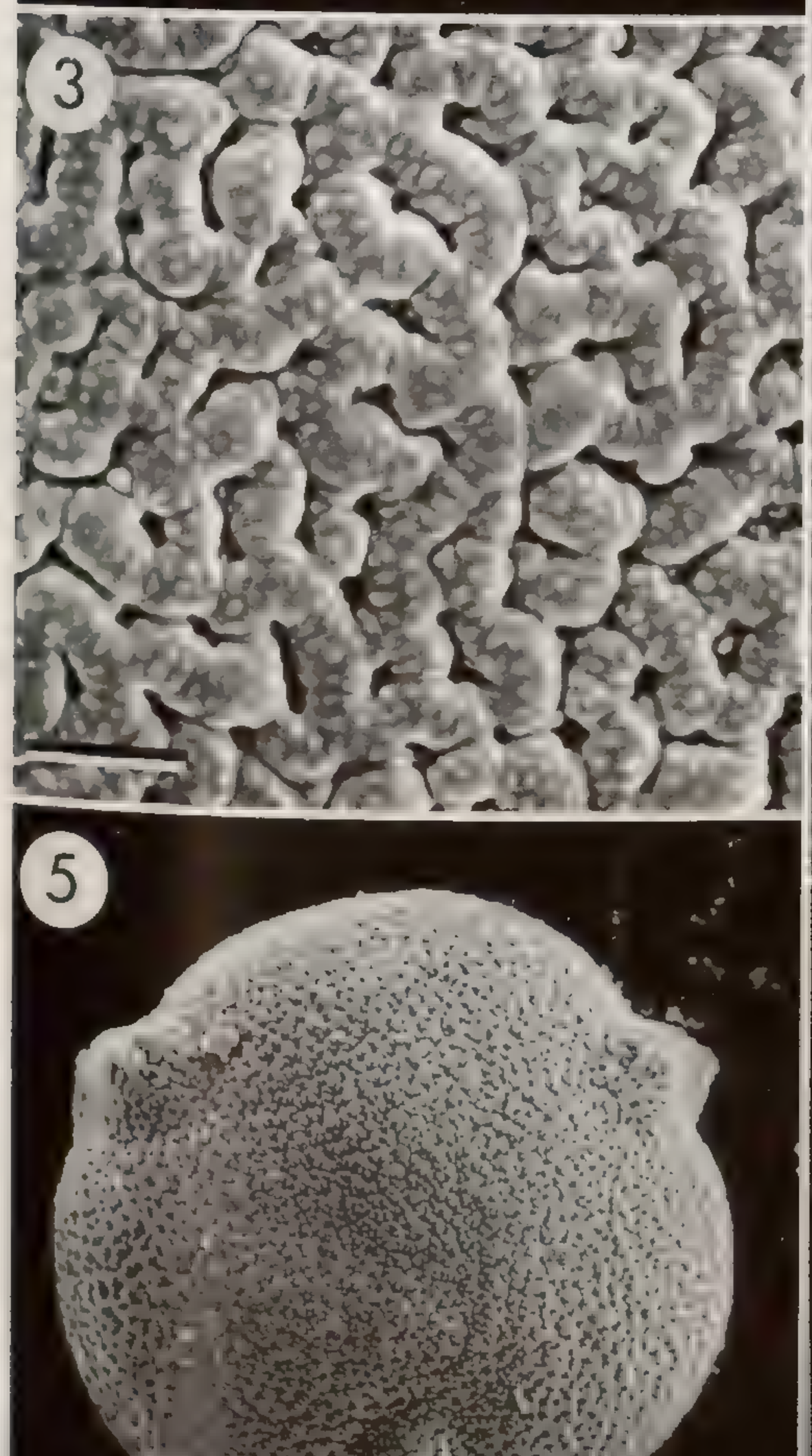
TABLE 1. Continued.

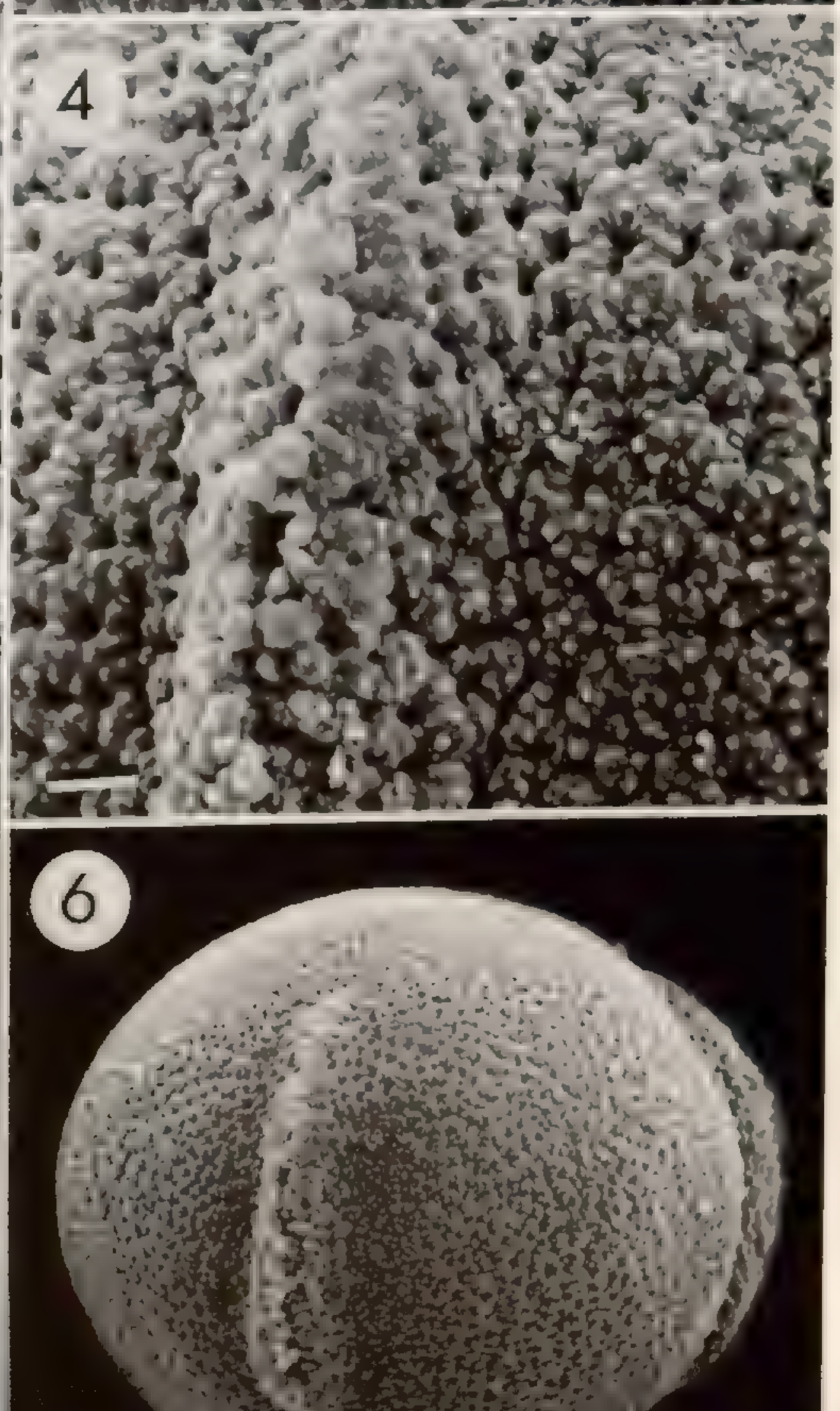
Species	Collection	Location		P Axis	E Axis	P E
Romanoa tamnoides (Adr. Juss.) A. Radcliffe-Smith	*Webster et al. 25436*, DAV	Brazil		53–55 (54.5)	58.5–62 (60)	0.91
Vigia serrata Vell.	*Bradem et al. 8376*, DAV	Brazil		36.5–46 (38.5)	46–55 (49)	0.79
V. serrata Vell.	*Hoehne 29250*, A	Brazil		ca. 32–35	ca. 42–51	
Tragiinae						
Acidoton nicaraguensis (Hemsley) Webster	*Ortiz 1104*, DAV	Nicaragua		34.5–39 (37)	39–46 (42)	0.88
A. nicaraguensis (Hemsley) Webster	*Steyermark & Davidse 116239*, DAV	Venezuela		39–41.5 (40)	39–48 (44)	0.91
A. urens Swartz	*Proctor 36826*, MO	Jamaica	*	37–46 (41.5)	39–48 (44)	—
A. microphyllus Urb.	*Leonard 5248*, US	Haiti	*	34–40.5 (37.5)	35–45.5 (40.5)	—
Cnesmone anisosepala (Merr. & Chun) Croiz.	*Lau 141*, UC	China	c	52–57.5 (55)	52–60 (56)	—
C. javanica Blume	*Morse 567*, NY	China	c	45.4–50.5 (47.5)	47–52 (49.5)	—
C. philippinensis (Merr.) Airy Shaw	*Ramos & Edaño 47087*, UC	Philippines	c	48.5–55 (52)	50.5–57.5 (54.5)	—
C. tonkinensis (Gagnep.) Croiz.	*Pételot 6521*, A	Vietnam	c	46–49.5 (47.5)	48.5–53 (51)	—
Megistostigma cordata Merr.	*Ramos 17591*, US	Philippines	c	48–58.5 (51)	48–58.5 (53)	—
M. malaccense Hook. f.	*Rahmat si Toroes 1389*, A	Indonesia	*	46–53 (48.5)	48.5–57.5 (52)	—
M. malaccense Hook. f.	*Burkhill & Haniff 15589*, MO	Malaysia	*	42.5–53 (48)	46–57.5 (52)	—
Pachystylidium hirsutum (Blume) Pax & K. Hoffm.	*Clemens 1748*, UC	Philippines		27.5–32 (30.5)	30–35.5 (33)	0.92
P. hirsutum (Blume) Pax & K. Hoffm.	*Ramos & Edaño 49201*, UC	Philippines		31–33.5 (32)	34.5–39 (36.5)	0.88
Platygyna hexandra (Jacq.) Muell. Arg.	*Howard et al. 81*, A	Cuba	*	—	37–44 (40)	—
P. hexandra (Jacq.) Muell. Arg.	*Jack 7146*, US	Cuba	*	35–41.5 (38.5)	37.5–44 (41)	—
P. leonis Alain	*Léon 12176*, DAV	Cuba	*	30–32 (32)	30–34.5 (32.5)	—
P. parvifolia Alain	*Schafer 1427*, NY	Cuba	*	30–39 (34.5)	35–40 (38.5)	—
Tragia adenanthera Baill.	*Tanner 672*, UC	Tanzania		31–39 (34.5)	34.5–46 (39)	0.88
T. bailloniana Muell. Arg.	*Cowan 2692*, DAV	Mexico		53–57.7 (56)	60–66.5 (62.5)	0.90

TABLE 1. Continued.

Species	Collection	Location		P Axis	E Axis	P/E
T. capensis Thunb.	*Ecklon & Zeyher s.n.*, US 1170932	South Africa		27.5–32 (31)	30–37 (35)	0.89
T. capensis Thunb.	*Kuntze s.n.*, NY	South Africa	a	23–30 (26)	27.5–33.5 (29.5)	0.88
T. chlorocaulon Baill.	*Eiten & Eiten 4285*, US	Brazil		30–35 (32.5)	34–43 (38.1)	0.85
T. cordifolia Vahl	*Webster s.n.*, DAV	Kenya		30–37 (34)	37–43.5 (39)	0.88
T. hispida Willd.	*Nicolson 2991*, US	India		36.5–40.5 (38)	41.5–45.5 (43.5)	0.87
T. involucrata L.	*Nicolson et al. HFP173*, US	India		30–34 (31.5)	34–40 (36)	0.87
T. ivohibeensis Leandri	*Humbert 3387*, DAV	Madagascar		41.5–46 (43.5)	44–55 (48)	0.91
T. lessertiana (Baill.) Muell. Arg.	*Webster 24119*, DAV	Surinam	*	—	46–53 (49)	—
T. mexicana Muell. Arg.	*Tuerckheim 7664*, US	Guatemala		30–35 (33)	35–40.5 (38)	0.87
T. novae-hollandiae Muell. Arg.	*Dovey B56*, UC	Australia		33.5–38 (36)	39–45 (41)	0.88
T. pacifica McVaugh	*McVaugh 21006*, DAV	Mexico		27.5–32 (30)	33.5–38 (35.5)	0.85
T. peltata Klotzsch	*dos Santos 1551*, DAV	Brazil		24–26.5 (25)	27.5–34.5 (30)	0.83
T. polyandra Vell.	*Bresolin 629*, US	Brazil		31–36.5 (33.5)	36.5–31.5 (38.5)	0.87
T. ramosa Torr.	*Ferris & Bacigalupui 8136*, DAV	U.S.A.		25.5 32 (28)	30–37 (32)	0.88
T. scandens (Baill.) Muell. Arg.	*Humbert 13741*, P	Madagascar		31–37.5 (33)	34–41.5 (38.5)	0.86
T. sellowiana (Klotzsch) Muell. Arg.	*Webster 25463*, DAV	Brazil	*	—	48.5–57.5 (54)	—
T. smallii Shinners	*Curtiss s.n.*, US	U.S.A.		35–39 (37)	37.5–44 (40.5)	0.92
T. tristis Muell. Arg.	*Anderson 9117*, DAV	Brazil		32–41.5 (37)	39–48 (43.5)	0.85
T. urens Small	*Norris 759*, DAV	U.S.A.		32–37 (34)	34.5–43.5 (38)	0.89
T. volubilis L.	*Webster & Proctor 5325*, DAV	Jamaica		25.5–27.5 (27)	30–33.5 (31)	0.87
Tragiella natalensis (Sond.) Pax & K. Hoffm.	*Mearns 295*, NY	Kenya		39–46 (42.5)	43.5–50.5 (46.5)	0.91
T. natalensis (Sond.) Pax & K. Hoffm.	*Mearns 295*, NY	Kenya	a	33.5–39 (36.5)	38–43 (39.5)	0.92

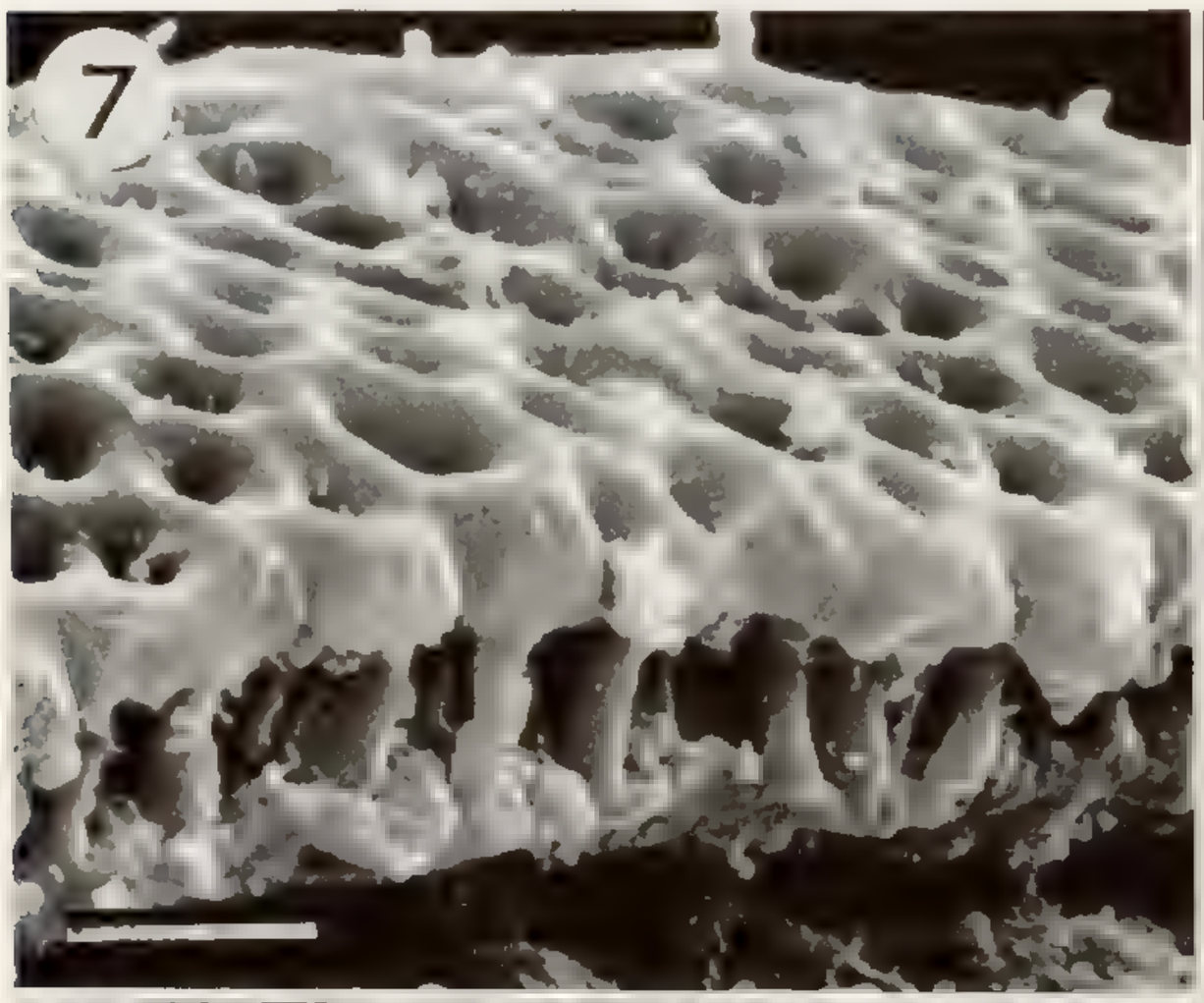


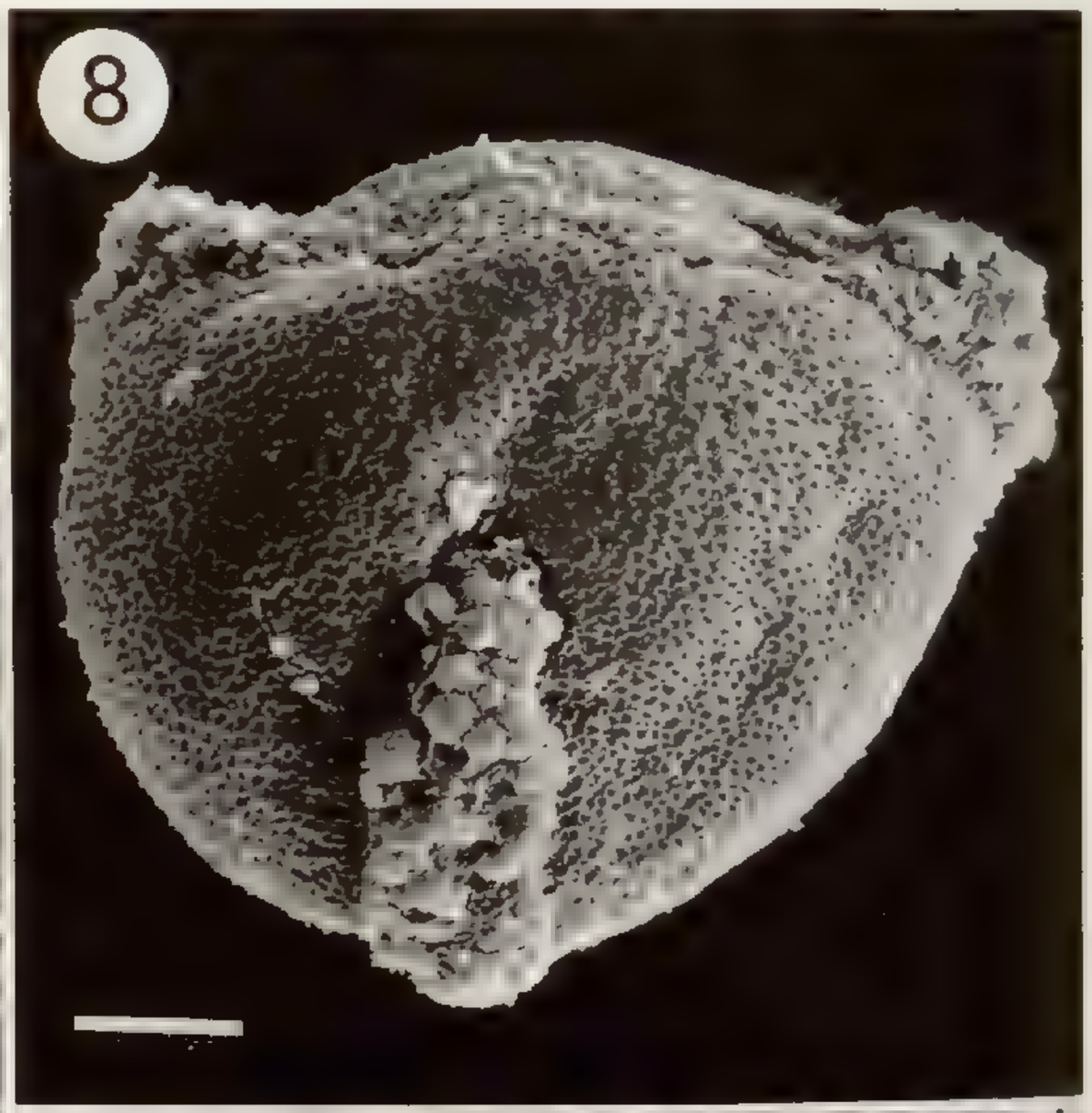


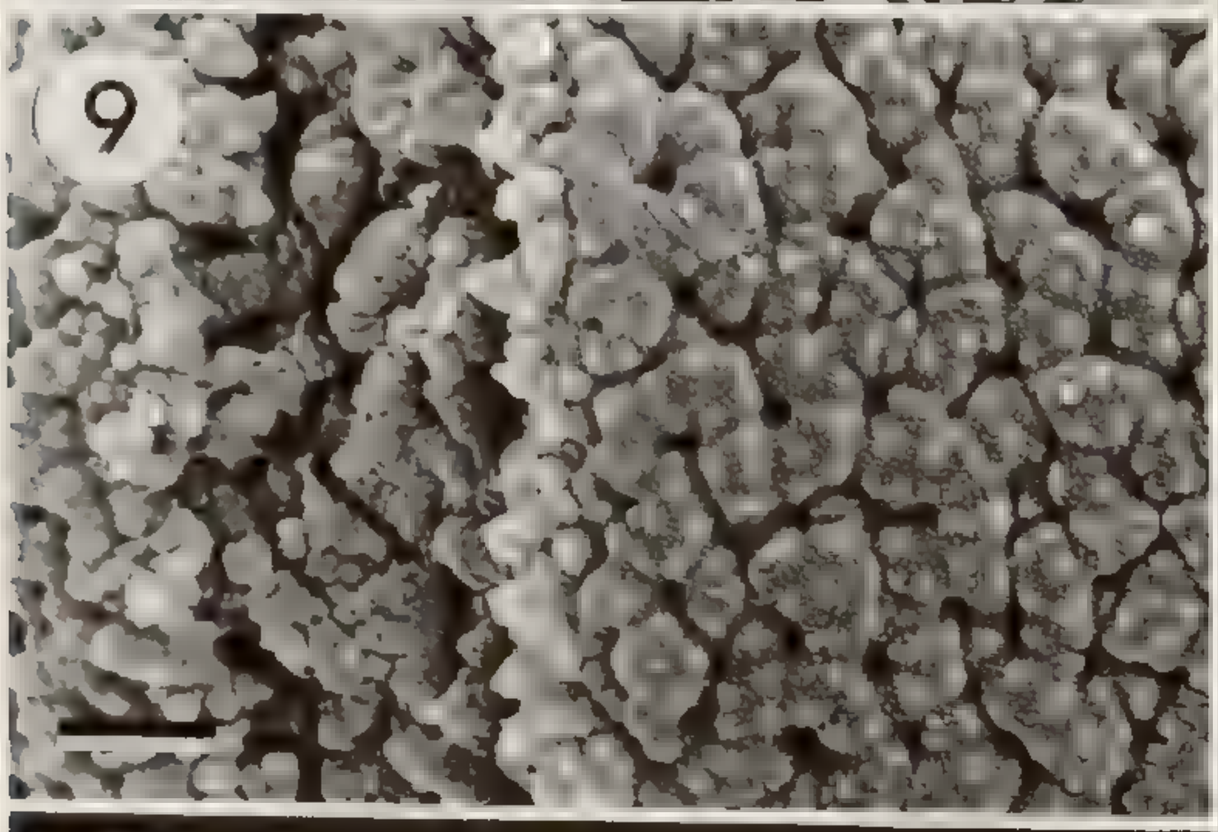


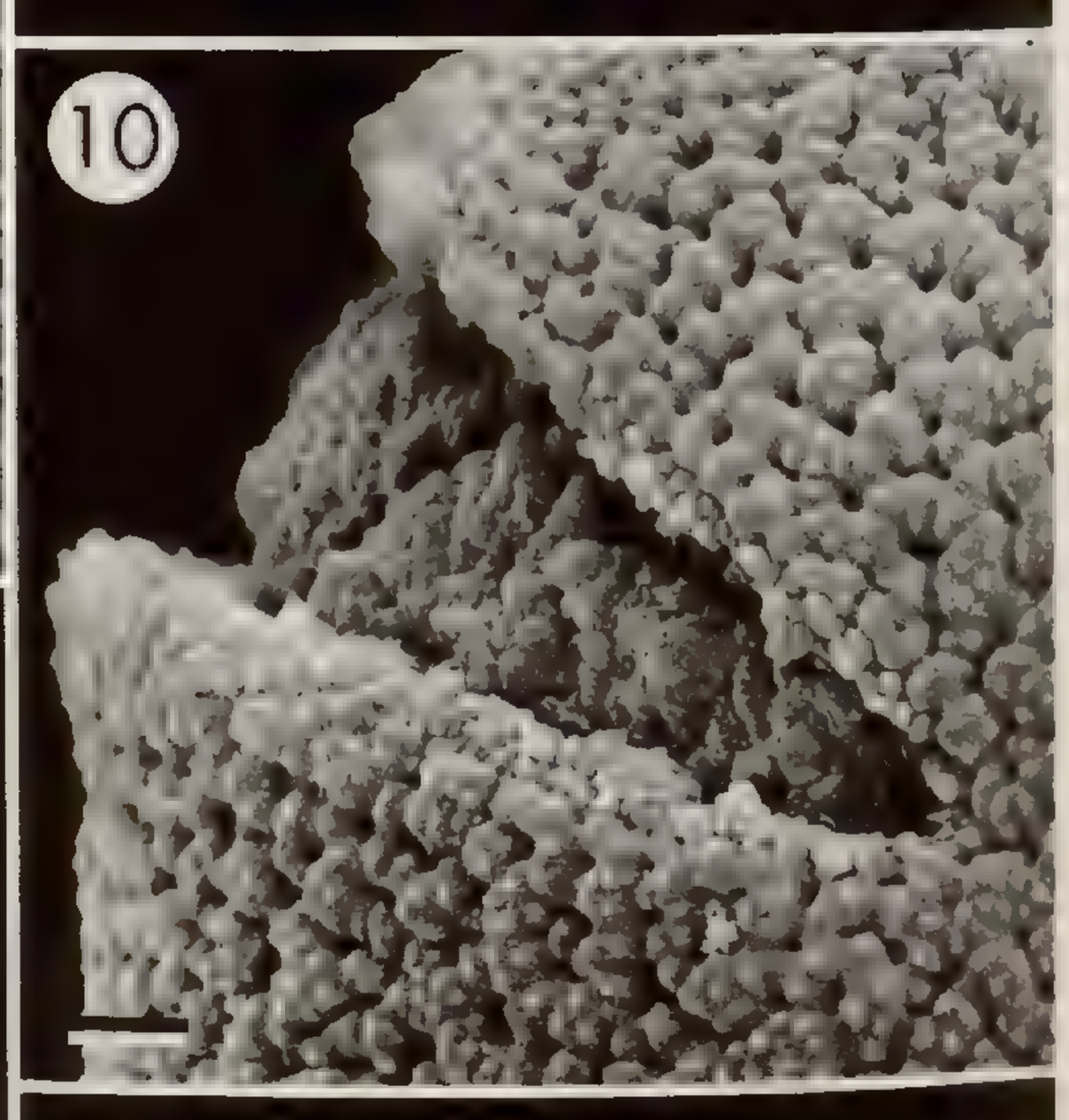
FIGURES 1–6. Scanning electron micrographs of pollen of *Angostyles* and *Astrococcus* (subtribe Plukenetiinae). 1–3. *Angostyles longifolia*. – 1. Polar view. – 2. Close-up of colpus. – 3. Exine sculpture. 4–6. *Astrococcus cornutus*. – 4. Close-up of colpus. – 5. Polar view. – 6. Equatorial view. Scale bar: = 10 μm in Figs. 1, 5, 6; = 5 μm in Fig. 2; = 2 μm in Figs. 3, 4.

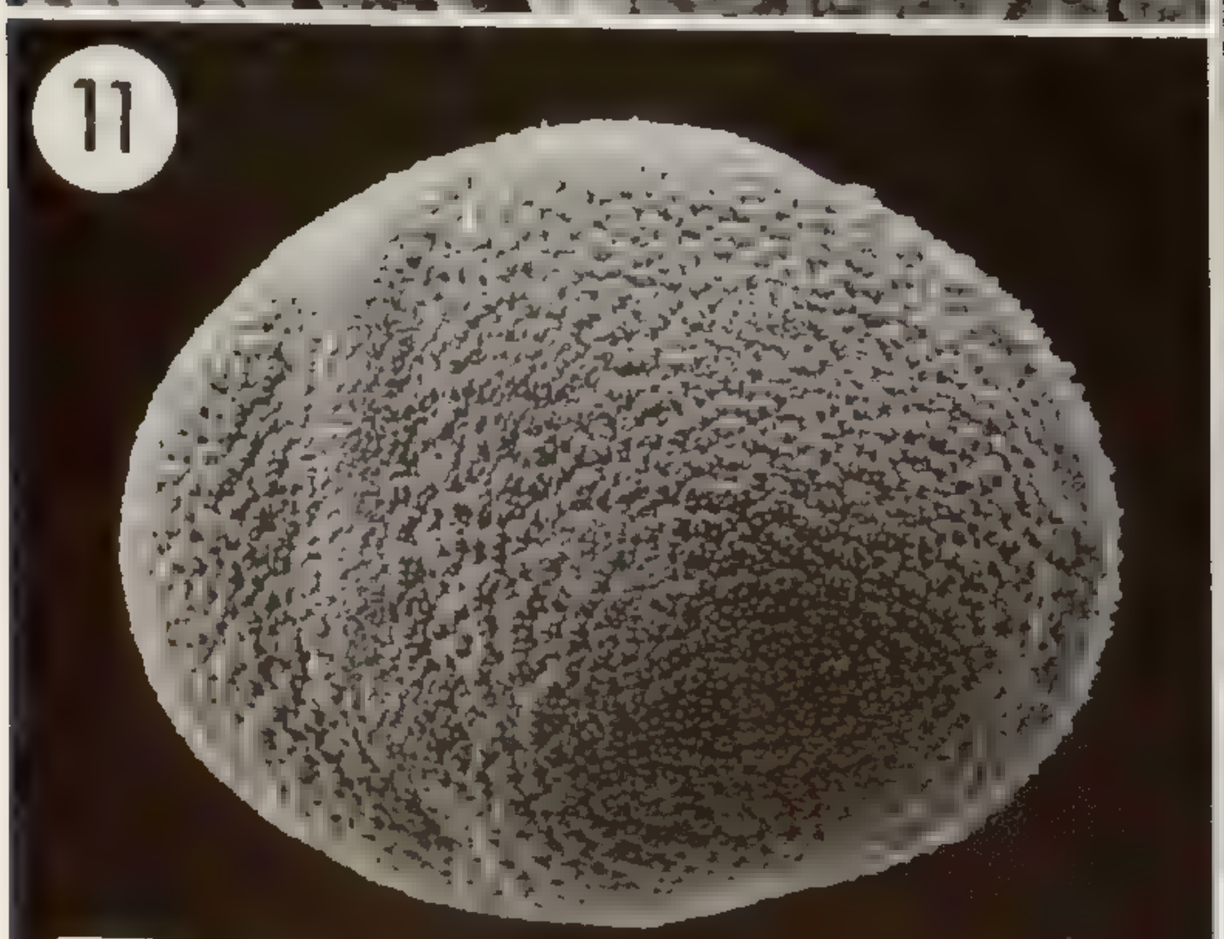
[1] Voucher information is in Table 1 unless given in the caption.

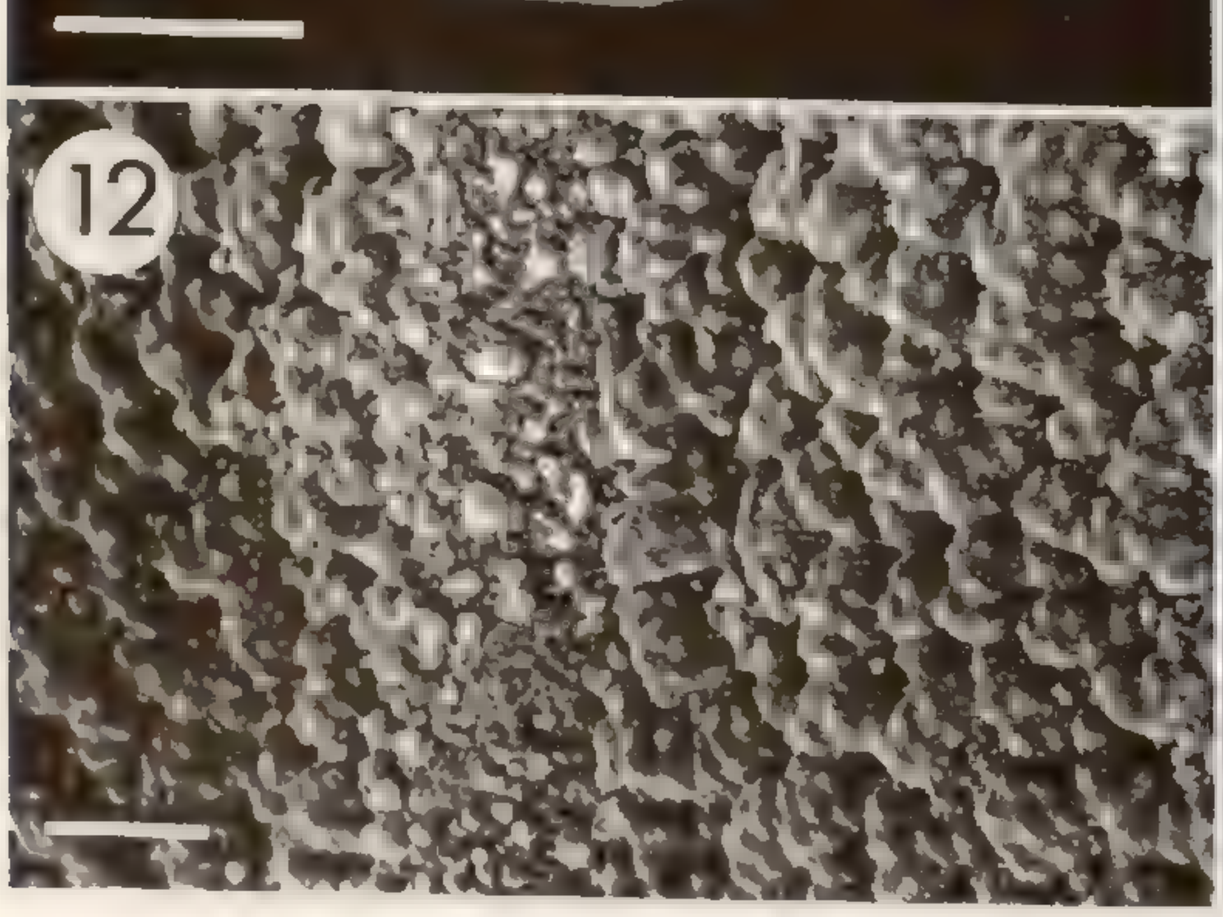












FIGURES 7–13.[3] Scanning electron micrographs of pollen of *Eleutherostigma* and *Haematostemon* (subtribe Plukenetiinae). 7–8. *Eleutherostigma lehmannianum*.—7. Exine structure of mesocolpium of fragmented grain.—8. Oblique view. 9–13. *Haematostemon coriaceus*.—9. Close-up of colpus in equatorial view lacking a continuous

and a total of 55 species were examined (Table 1). Pollen of *Sphaerostylis*, a small genus of vines endemic to Madagascar, and one section of *Tragia* endemic to Madagascar, *Agirta* Baill., was not available.

Results—Subtribe Plukenetiinae

Angostyles (Figs. 1–3). A monotypic genus of small trees known only from the Rio Negro region of Amazonian Brazil.

Pollen suboblate (P/E = 0.87), 54 μm P × 62 μm E, tricolpate; amb subcircular to obscurely obtuse-triangular; colpus narrow and short, margins uneven; exine tectate-perforate, 1–1.5 μm thick, uniformly thickened; tectum very finely foveolate-rugulate, fragmented and irregularly finely gemmate at colpus margin, rugae with evenly spaced microverrucae, intervening perforations narrow, sinuous to sometimes small and circular.

Astrococcus (Figs. 4–6). A monotypic genus of shrubs or small trees in the upper Rio Negro region of Venezuela and Brazil.

Pollen suboblate to oblate-spheroidal (P/E = 0.88), 48 μm P × 54.5 μm E, tricolpate; amb subcircular to obscurely obtuse-triangular; colpus very narrow and short, sometimes covered with an unbroken sexinous membrane, margins uneven; exine tectate-perforate, 1.5–2 μm thick, becoming thicker, ca. 2.5–3 μm, and distinctly raised at colpus margin, with upper and lower exine layers separating forming an elongate chamber in the vicinity of the colpus; tectum very finely foveolate-rugulate, fragmented and irregularly, finely gemmate at colpus margin, rugae with 2(–3) rows of evenly spaced microverrucae, intervening perforations very narrow, sinuous to small and circular particularly near the colpus.

A continuous unbroken sexine may sometimes be present over the apertures as in pollen of *Haematostemon* (Figs. 11, 12; refer to description and discussion under *Haematostemon*).

Eleutherostigma (= *Plukenetia*) (Figs. 7, 8). A monotypic genus of lianas of premontane forest in Colombia and Ecuador, its single species now treated as a species of *Plukenetia*, *P. lehmanniana* (Pax & K. Hoffm.) Huft & L. J. Gillespie.

Pollen oblate-spheroidal (P/E = 0.89), 50.5 μm P × 56.5 μm E, tricolpate; amb obtuse-triangular, angulaperturate; colpus broad with ends often indistinct, margins uneven and jagged; exine tectate-perforate, 2–2.5 μm thick, somewhat thinner at colpus margin; tectum foveolate, surface smooth.

Haematostemon (Figs. 7–13). Two species of shrubs or small trees in Guyana and Amazonas, Venezuela, both examined.

Pollen suboblate to oblate-spheroidal (P/E = 0.86–0.89), 35–44 μm P × 40.5–49.5 μm E, tricolpate; amb subcircular; colpus narrow, sometimes covered with an unbroken sexinous membrane, margins uneven; exine tectate-perforate, 1.5–2 μm thick, becoming thicker, 3–3.5 μm, at colpus margin, with upper and lower exine layers separating forming an elongate chamber in the vicinity of the colpus; tectum very finely foveolate-rugulate, becoming fragmented and irregularly gemmate at colpus margin, rugae with (1–)2(–3) rows of evenly spaced microverrucae, intervening perforations narrow, sinuous to small and circular; apertural sexine, when present, densely and irregularly scabrate.

Grains within a single SEM preparation have apertures that appear to have a sexine that is continuous (Figs. 9, 10) or very fragmented (or sometimes absent) (Figs. 7, 8, 11, 12) over the apertures. This difference may perhaps be due to degree of rehydration or tolerance to treatment with acetone or sonication, resulting in some grains having a ruptured or degraded apertural sexine.

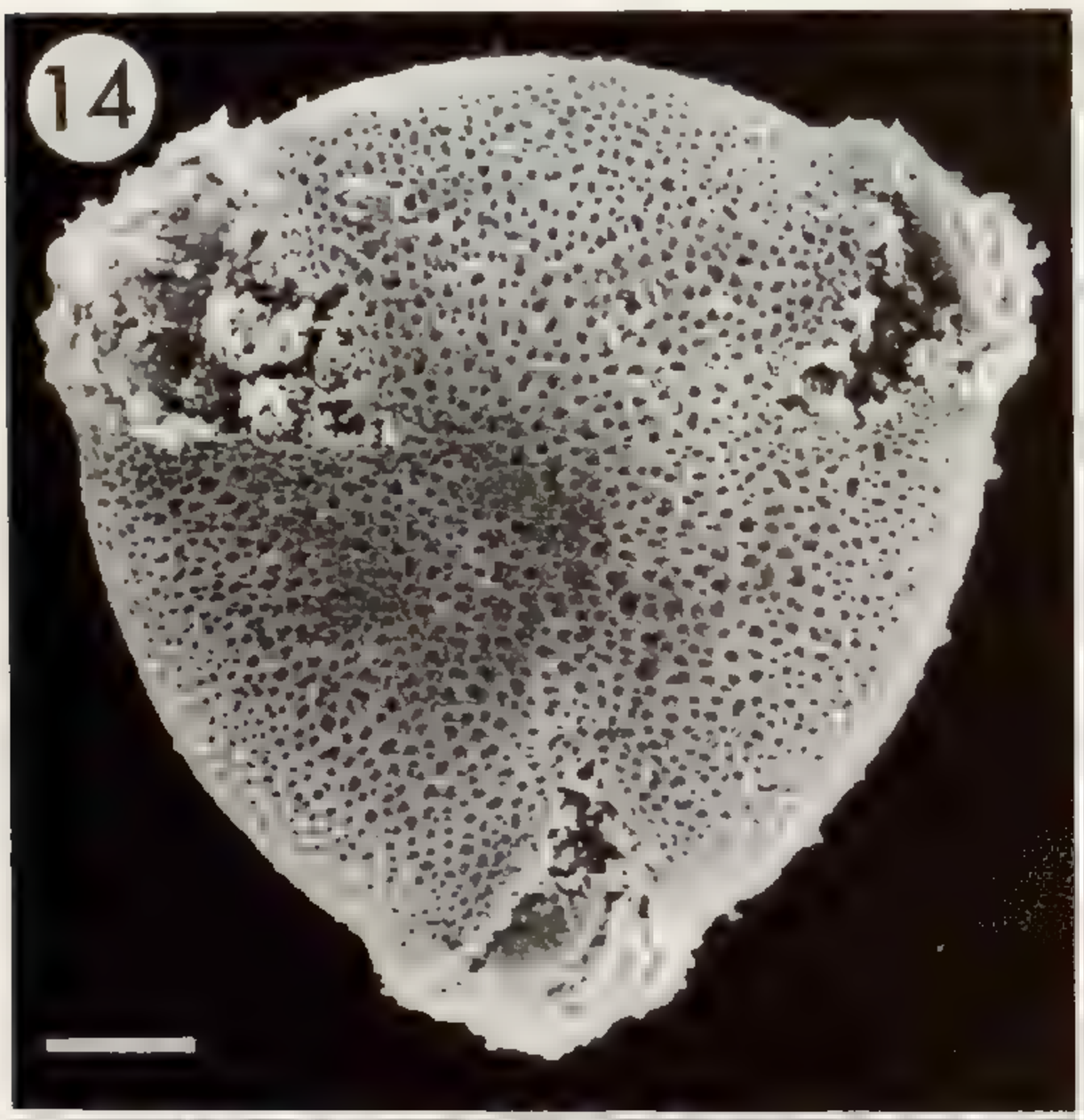
Plukenetia (Figs. 14–24). A genus of 16 species of twining vines and lianas distributed pantropically with one species in Asia, four in Africa and Madagascar, and 11 in the Neotropics (note that the two species previously treated as species of *Eleutherostigma* and *Vigia* are included in the species count but are described separately). The 13 species examined may be divided into two pollen types based on tectum morphology.

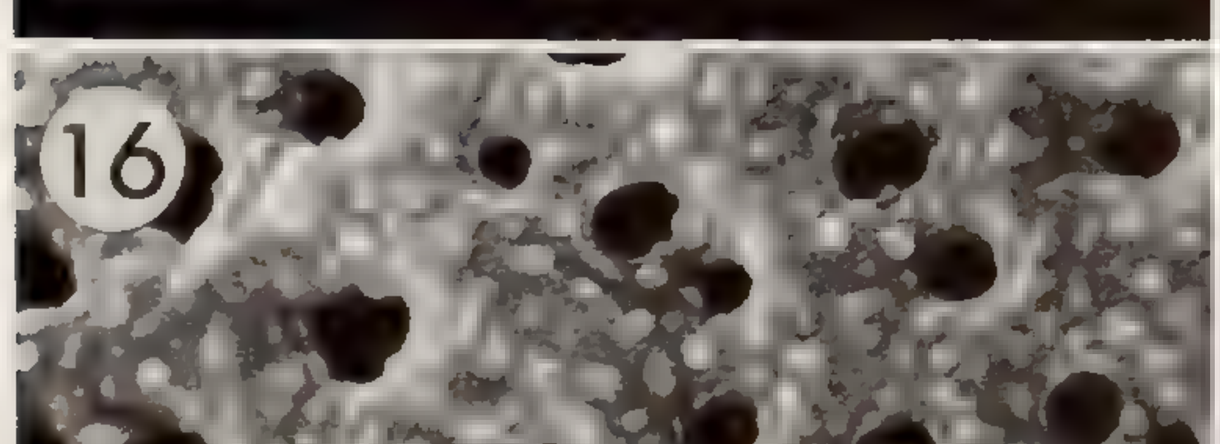
Type 1 (Figs. 14–19). Pollen suboblate to oblate-spheroidal (P/E = 0.80–0.89), 35–56 μm P × 42.5–64.5 μm E, tricolpate; amb obtuse-triangular to subcircular, angulaperturate; colpus broad with margins very uneven and jagged; exine tectate-perforate, 1.5–4 μm thick; tectum foveolate with foveolae sometimes becoming smaller at aperture margin, surface smooth or scabrate (e.g., *P. stipellata*).

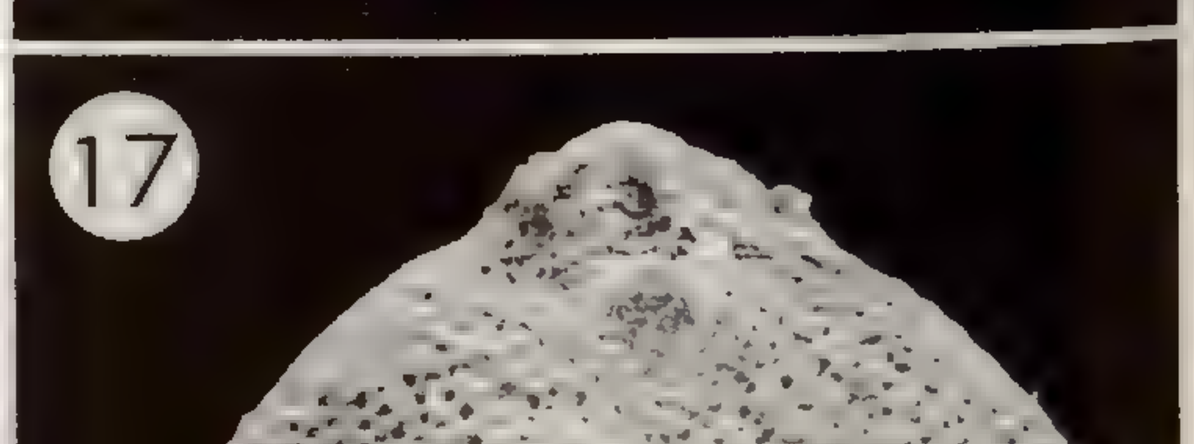
Of the seven species included in Type 1, the

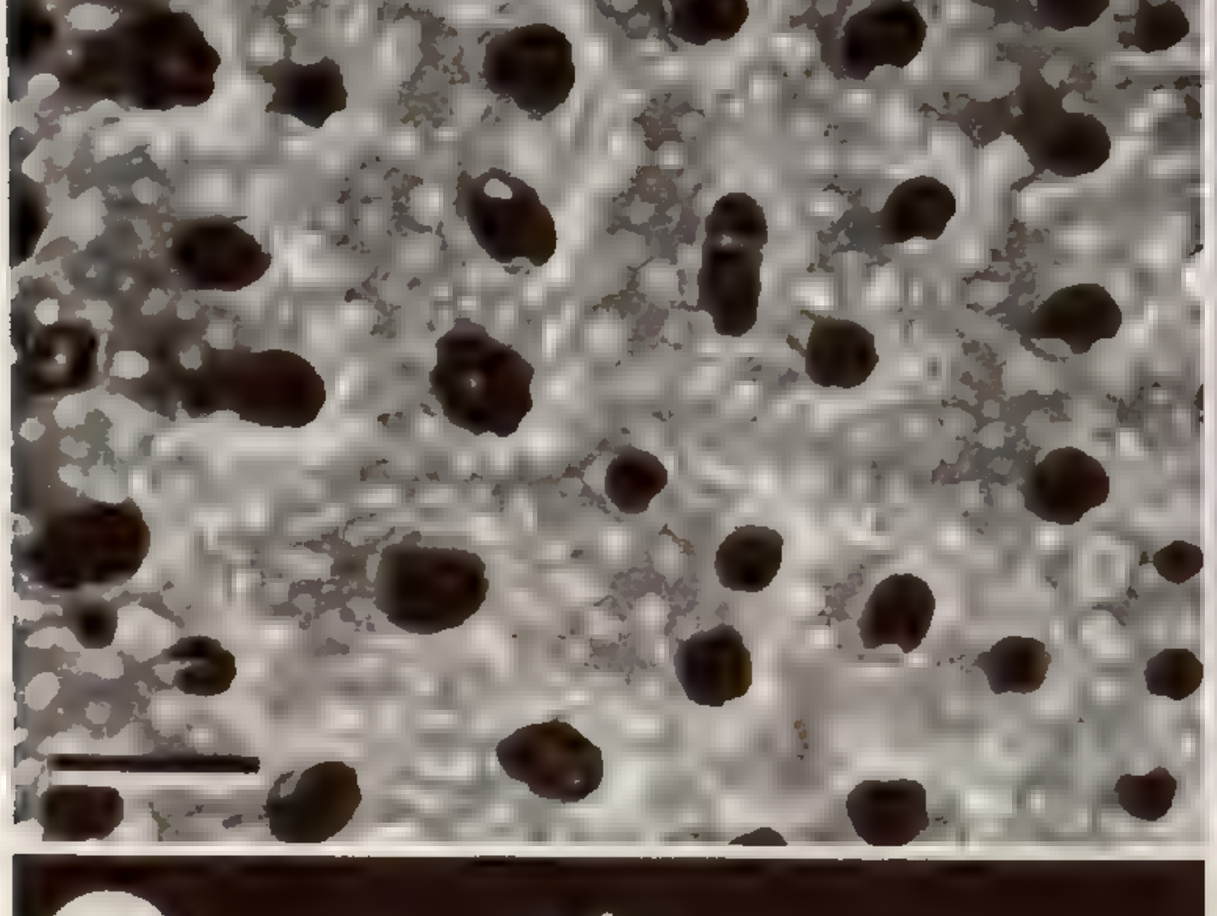
←

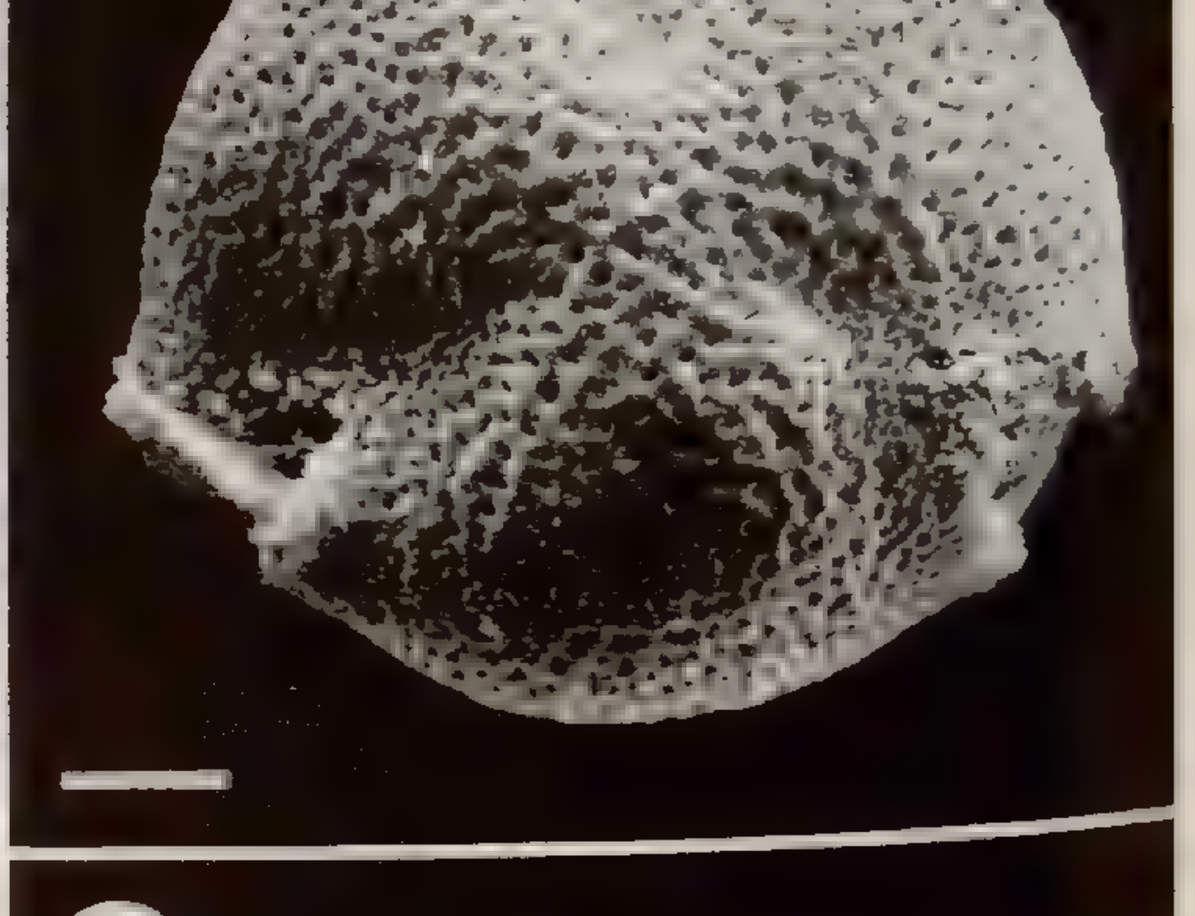
apertural sexine.—10. Close-up of colpus of grain in Fig. 13; note lack of an apertural sexine.—11. Equatorial view.—12. Close-up of colpus of grain in Fig. 11; note presence of sexine covering aperture.—13. Polar view of grain lacking a distinct apertural sexine. Scale bar: = 10 μm in Figs. 8, 11, 13; = 2 μm in Figs. 7, 9, 10, 12.



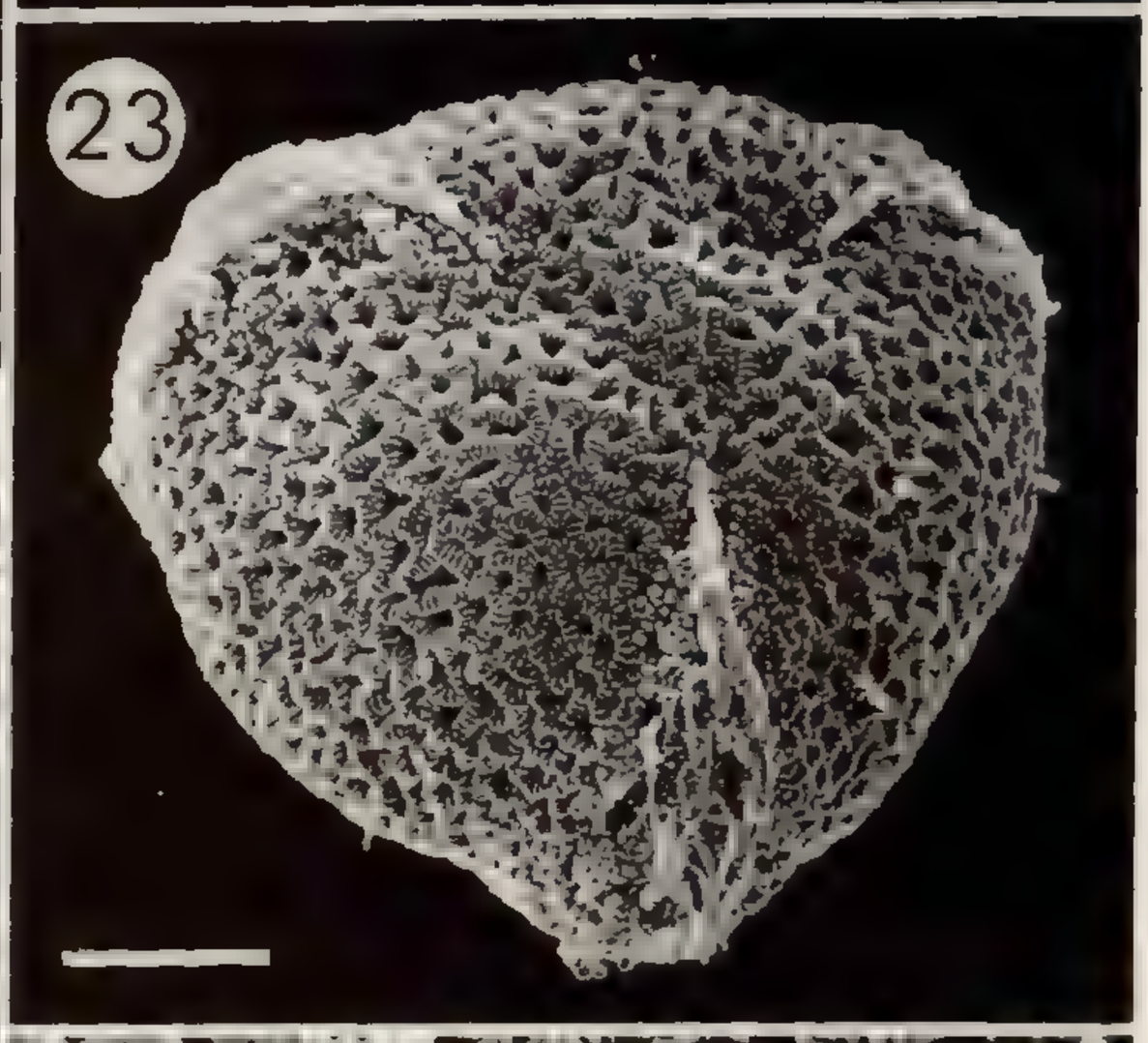


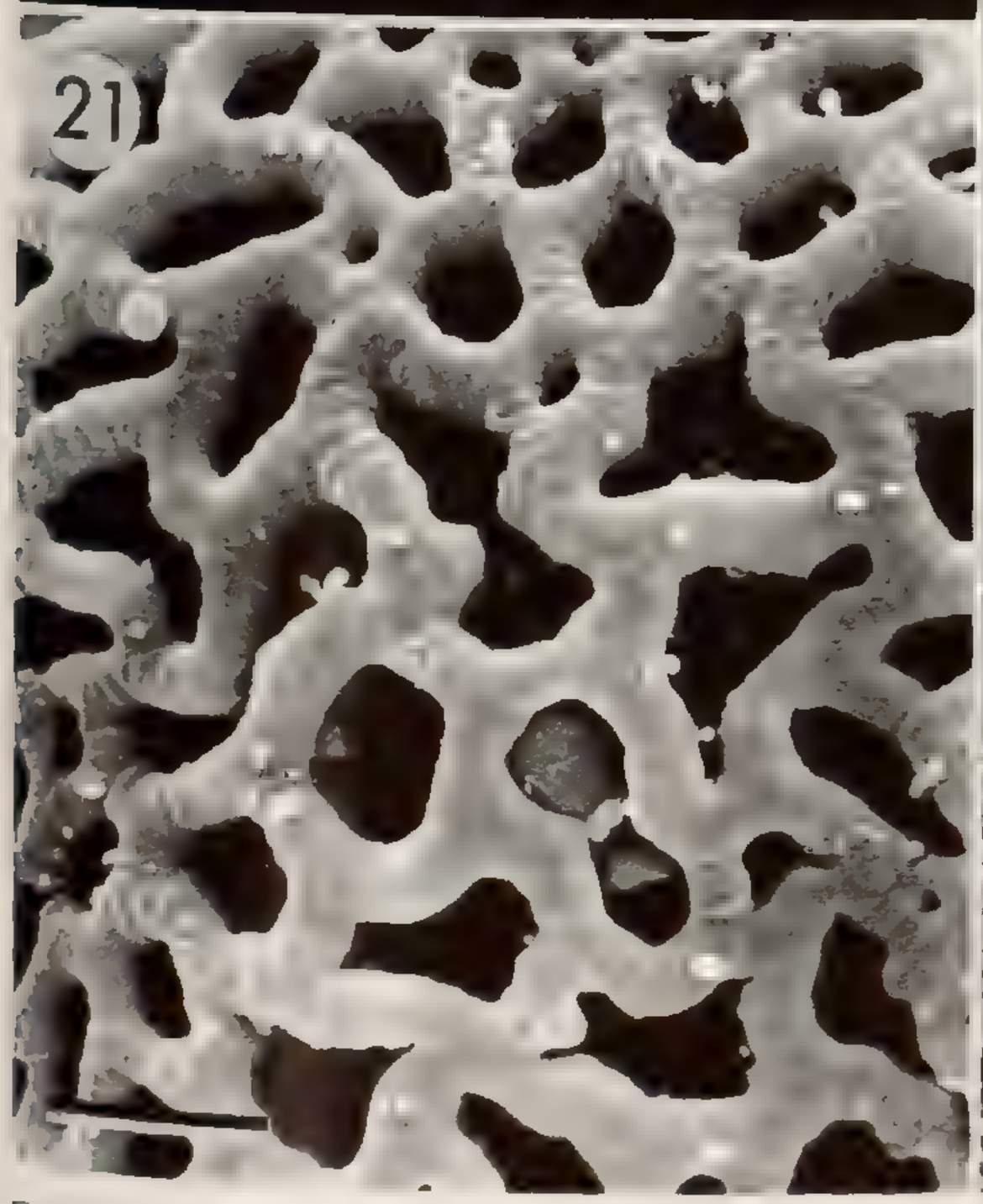






FIGURES 14–19. Scanning electron micrographs of pollen of *Plukenetia* (pollen Type 1). 14–16. *P. stipellata* 14. Polar view. —15. Equatorial view. —16. Exine sculpture. —17. Polar view of *P. polyadenia*. —18. Polar view of *P. africana* (Wild 5062 MO). —19. Equatorial view of acetolyzed grain of *P. conophora*. Scale bar: = 10 μm in Figs. 14, 15, 17–19; = 2 μm in Fig. 16.



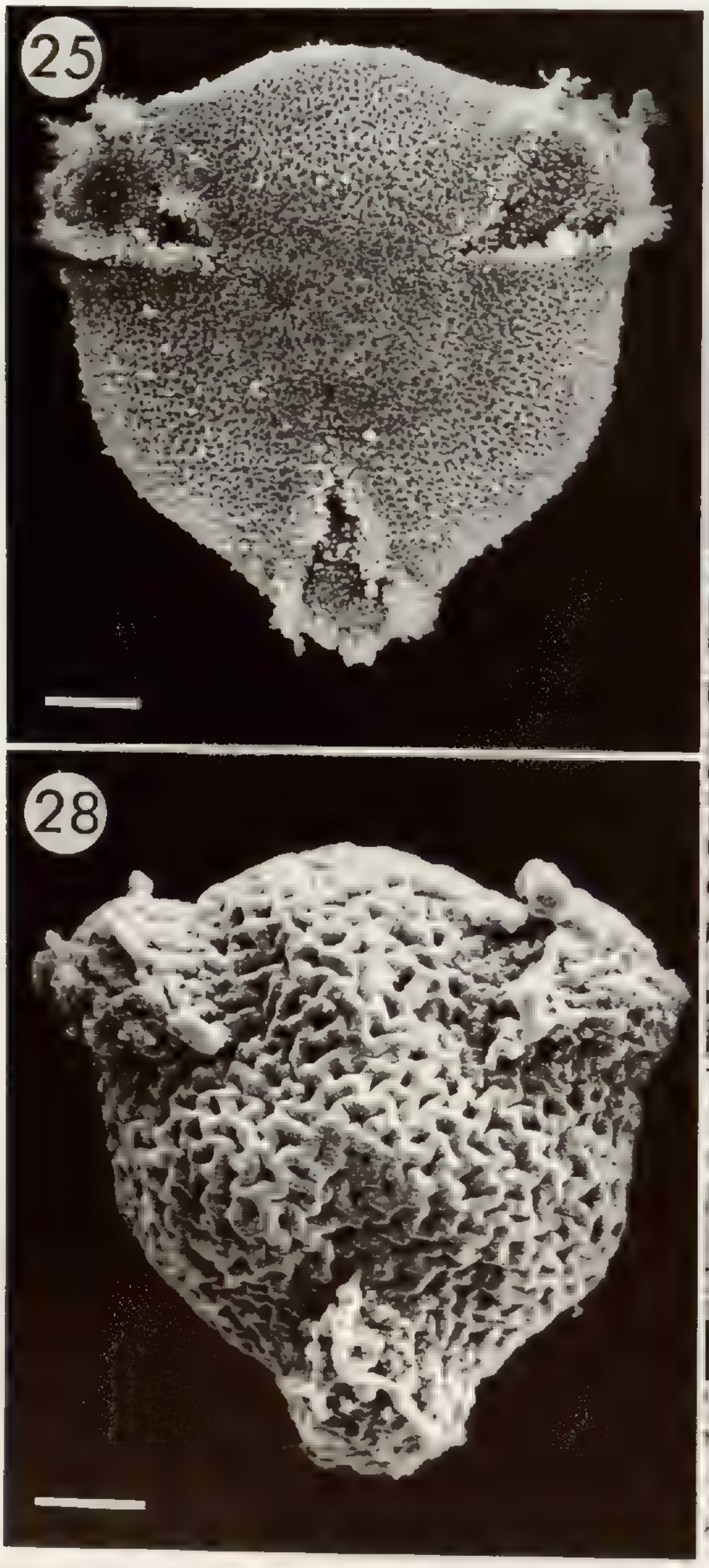


FIGURES 20–24.[3] Scanning electron micrographs of pollen of *Plukenetia* (pollen Type 2). 20–22. *P. loretensis* (Maguire & Politi 27371 US).—20. Polar view.—21. Exine sculpture.—22. Equatorial view. 23–24. *P. penninervia* (Standley 56708 A).—23. Oblique view.—24. Close-up of colpus and exine sculpture. Scale bar: = 10 μm in Figs. 20, 22, 23; = 5 μm in Figs. 21, 24.

New World species, *Plukenetia polyadenia* (Fig. 17), *P. stipellata* (Figs. 14–16), and *P. volubilis* have large pollen grains (57–69 μm E) with an amb usually obtuse-triangular and an exine 2–4 μm thick that becomes gradually thinner at the colpus margin. The Old World species, *P. africana* (Fig. 18), *P. conophora* (Fig. 19), *P. corniculata*, and *P. madagascariensis* have medium-sized pollen grains (41–50 μm E) with a subcircular amb and an exine 1.5–2.5 μm that is mostly uniformly thick or sometimes thickened at the colpus margin.

Type 2 (Figs. 20–24). Pollen suboblate (P/E = 0.78–0.85), 32–55 μm P × 41–66.5 μm E, tricolpate; amb obtuse-triangular, angulaperturate; colpus broad with margins very uneven and jagged; exine semitectate-reticulate, 2.5–4.5 μm thick; muri usually crenate (i.e., tranversely ridged), becoming fragmented and sometimes finely gemmate at colpus margin, lumina often smaller near colpus margin.

Of the six species included in Type 2, *Plukenetia brachybotrya* and *P. loretensis* (Figs. 20–22) have



FIGURES 25–29. Scanning electron micrographs of pollen of *Romanoa* and *Vigia* (subtribe Plukenetiinae). 25–27. *Romanoa tamnoides*. —25. Polar view. —26. Close-up of colpus of grain less expanded than in Fig. 25. —27. Exine sculpture. —28. Polar view of *Vigia serrata* (Brademet al. 8376 DAV). —29. Close-up of colpus margin (at left) and exine sculpture of *V. serrata* (Hoehne 29250 A). Scale bar: = 10 μm in Figs. 25, 26, 28; = 5 μm in Figs. 27, 29.

large grains (60–76 μm E) with an exine ca. 4–4.5 μm thick, while *P. multiglandulosa*, *P. penninervia* (Figs. 23, 24), *P. supraglandulosa* (Gillespie, 1933: figs. 7, 8), and *P. verrucosa* have medium-sized grains (39–51 μm E) with an exine ca. 2.5–3 μm. Pollen of both Type 1 and Type 2 frequently appear to have small sexinous fragments on the apertural membrane (e.g., Figs. 14, 15, 18, 20, 22).

Romanoa (Figs. 25–27). A monotypic genus of twining woody vines endemic to southeastern Brazil.

Pollen oblate-spheroidal (P/E = 0.91), 54.5 μm P × 60 μm E, tricolpate; amb obtuse-triangular, angulaperturate; colpus broad, margins very uneven and jagged; exine tectate-perforate, 3–3.5 μm thick, gradually thinning toward the colpus margin; tectum fossulate-foveolate, surface scabrate.

Vigia (= *Plukenetia*) (Figs. 28, 29). A mono-

typic genus of vines and lianas of southeastern Brazil, now treated as a species of *Plukenetia*, *P. serrata* (Vell.) L. J. Gillespie.

Pollen suboblate (P/E = 0.79), 38.5 μm P × 49 μm E, tricolpate; amb obtuse-triangular, angulaperturate; colpus broad with margins uneven; exine semitectate-reticulate, 2.5–3 μm thick, thinner at colpus margin; muri often crenate, becoming fragmented and finely gemmate at colpus margin.

Elongate strands of sexine were observed near the colpus margin on many grains of both collections in SEM (Figs. 28, 29), but were not visible in LM.

Results—Subtribe Tragiinae

Acidoton (Figs. 30–35). Five species of shrubs in the West Indies, Central America, and northern South America. Three species were examined. Two pollen types may be distinguished based on aperture presence and exine structure.

Type 1 (Figs. 30–32). Pollen oblate-spheroidal (P/E = 0.88–0.91), 37–40 μm P × 42–44 μm E, tricolpate; amb subcircular or obscurely obtuse-triangular; colpus narrow with irregularly shaped islands of sexine, margin uneven and often indistinct; exine tectate-perforate, ca. 1.5 μm thick, uniformly thickened; tectum finely and irregularly foveolate-reticulate, lumina round to slitlike and usually narrower than the muri, muri often broken and incomplete, surface microspinulose; apertural sexine islands with surface similar to nonapertural sexine, but more irregular.

Acidoton nicaraguensis (synonym: *A. venezolanus*), the only species in Central and South America, has pollen of Type 1.

Type 2 (Figs. 33–35). Pollen spheroidal to ellipsoid-spheroidal, 37.5–41.5 μm S, 40.5–44 μm L, inaperturate; outline circular to broadly elliptic; exine tectate-rugulate, ca. 1.5 μm thick; rugae short to elongate, sometimes appearing beaded with slight constrictions at usually regular intervals, surface smooth, intervening perforations variable in width.

The two West Indian species examined belong to Type 2. *Acidoton microphyllus* (Fig. 35) appears to have more conspicuously beaded rugae than *A. urens* (Figs. 33, 34).

Cnesmone (Figs. 36–39). A genus of ca. 12 species of twining vines and lianas from southeastern China to the Philippines and Indonesia. Four species were examined.

Pollen spheroidal to ellipsoid-spheroidal, sometimes irregular in shape, 47.5–55 μm S, 49.5–56 μm L, weakly tricolpate; outline circular or elliptic, occasionally irregularly obtuse-triangular; aperture large, elliptic in shape with margins uneven, covered with exine approximately equal in thickness to the nonapertural exine, but having a fragmented sexine; exine tectate-perforate, 1–2 μm thick, uniformly thickened; tectum punctate (i.e., having very small foveolae) and microverrucate; apertural sexine fragmented with narrow fissures separating small, irregularly shaped islands, surface microverrucate and sometimes punctate.

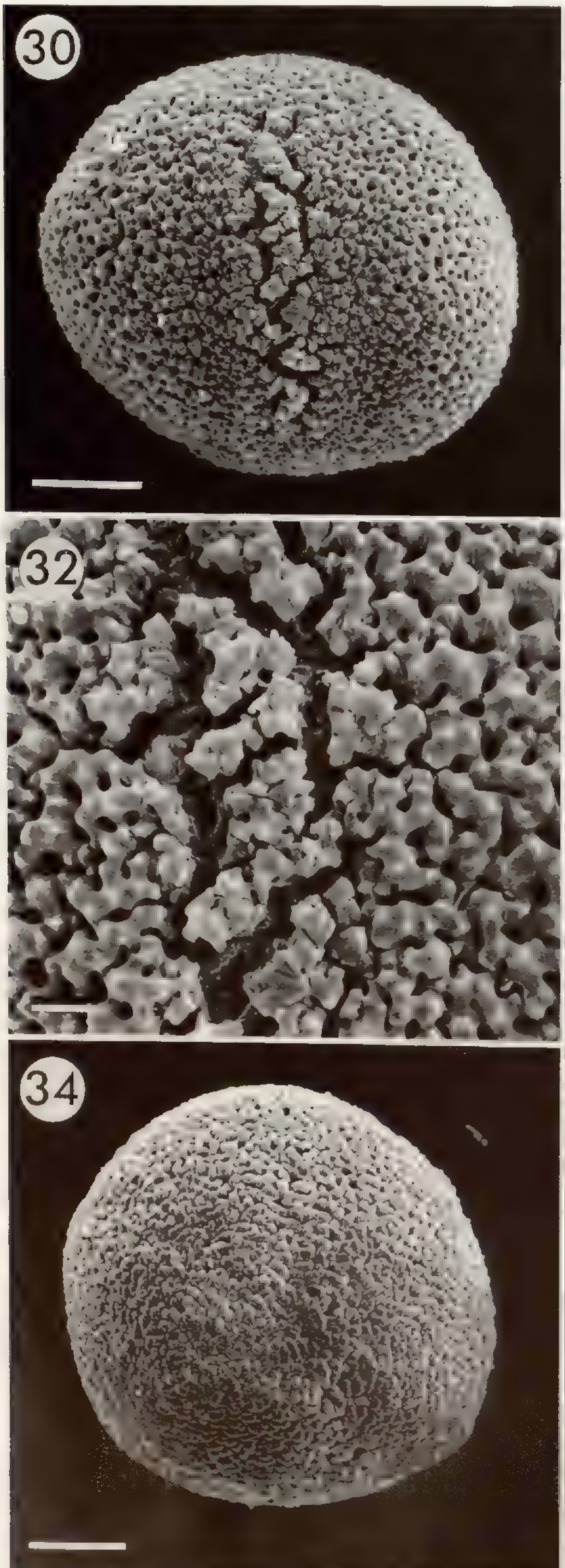
Although clearly visible under SEM, the apertures are usually not visible under LM (sometimes appearing as three less dense, more sculptured areas in optical cross section of nonacetolyzed grains, more frequently visible in acetolyzed grains). Therefore, even though the grain is aperturate, shortest and longest axes are given rather than polar and equatorial axes. The apertural sexine appears very similar to the nonapertural sexine, but is fragmented into irregularly shaped islands separated by usually narrow fissures. Typically, this weaker sexine forms three large, poorly defined colpi (Figs. 36, 39); however, apertural regions of some grains are more irregular and do not form distinct apertures (Fig. 37).

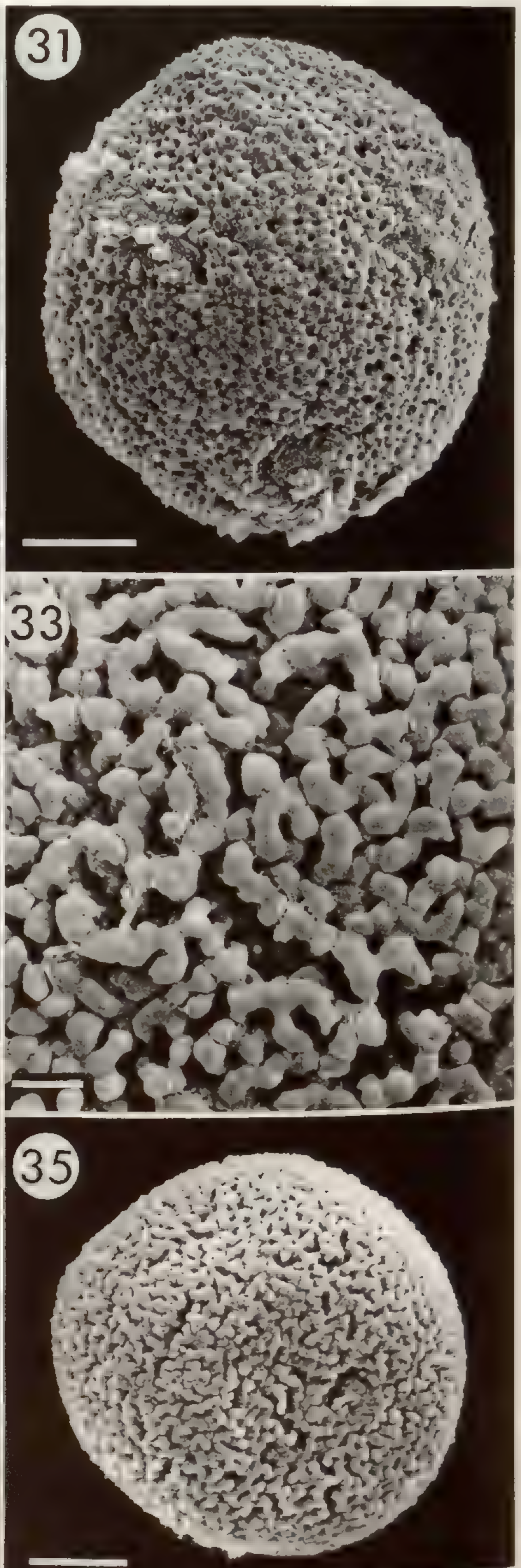
Megistostigma (Figs. 40, 41). Five species of twining vines and lianas from southeastern China to the Philippines and Indonesia. Two species were examined.

Pollen spheroidal to ellipsoid-spheroidal, 48–51 μm S × 52–53 μm L, weakly tricolpate, irregularly aperturate or sometimes inaperturate; outline circular or elliptic; apertural-like areas usually present, either 3(–4), large, elliptic apertures or irregularly shaped areas not forming distinct apertures; exine tectate-perforate, ca. 1 μm thick, uniformly thickened throughout; tectum punctate and microverrucate, surface often uneven; sexine of apertural-like areas fragmented into irregularly shaped islands separated by narrow branched fissures, surface microverrucate and sometimes punctate.

The areas of fragmented sexine are less dense, presumably weaker areas of exine that probably function in a manner similar to apertures. In *Megistostigma malaccense* this fragmented sexine may sometimes be absent or more commonly randomly distributed, sometimes but not always forming patterns such as rings (Figs. 40, 41, or similar to the atypical grain of *Cnesmone*, Fig. 37). In *M. cordata* these less dense areas are distributed either in the form of three (or sometimes four), large, poorly defined colpi as in *Cnesmone* (Figs. 36, 39) or in a more random pattern.

Pachystylidium (Figs. 42, 43). A monotypic genus of twining vines distributed from India to the Philippines and Indonesia.





FIGURES 30–35.[3] Scanning electron micrographs of pollen of *Acidoton* (subtribe Tragiinae). 30–32. *A. nicaraguensis* (Ortiz 1104 DAV).—30. Equatorial view.—31. Polar view.—32. Close-up of colpus and exine sculpture; note presence of sexine islands on the aperture. 33–34. *A. urens*.—33. Exine sculpture showing rugae separated by fossae of variable width.—34. Grain having fossae of mostly narrow width.—35. Grain of *A. microphyllus*. Scale bar: = 10 μm in Figs. 30, 31, 34, 35; = 2 μm in Figs. 32, 33.

Pollen oblate-spheroidal (P/E = 0.88–0.92), 30.5–32 μm P × 33–36.5 μm E, weakly triporate; amb subcircular to obtuse-triangular, angulaperturate; aperture circular to broadly elliptic, L/W ca. 1–1.5, covered with exine slightly thinner than the nonapertural exine, but with a fragmented sexine; exine tectate-perforate, 1.5–2 μm thick, uniformly thickened; tectum punctate, microverrucate; apertural sexine fragmented into small irregularly shaped islands separated by fissures, surface microverrucate and occasionally punctate.

Pollen grains are similar to those of *Cnesmone* (Figs. 36–39), but differ in their circular apertures (Fig. 42) that are usually visible under LM as areas of slightly thinner, more sculptured exine. In addition, the apertures may sometimes appear as depressed areas under SEM (Fig. 42, aperture on right).

Platygyna (Figs. 44–46). Seven species of twining woody vines endemic to Cuba. Three species were examined.

Pollen spheroidal or sometimes ellipsoid-spheroidal, 32–41 μm diam., inaperturate; outline circular to broadly elliptic, often irregularly so; exine tectate-perforate, 3–4 μm thick, uniformly thickened; tectum reticulate or rugulate with muri or rugae wider than the usually slitlike intervening perforations, surface smooth.

Platygyna hexandra (Fig. 44) and *P. leonis* (Fig. 45) have a reticulate tectum with broad muri, whereas *P. parvifolia* (Fig. 46) has a rugulate tectum.

Tragia (Figs. 47–74). A genus of ca. 130 species of herbs, twining vines, and shrubs found in warm temperate and tropical regions around the world, particularly abundant in the New World and Africa. Twenty-one species belonging to two subgenera and seven sections were examined. Seven pollen types may be distinguished based on aperture condition, aperture morphology and exine structure; these types correspond closely with the infrageneric classification system.

Tragia* sect. *Bia (Figs. 47–50). Neotropical section of six species, of which *T. lessertiana* and *T. sellowiana* were examined here.

Pollen spheroidal or rarely ellipsoid-spheroidal, 49–54 μm diam., inaperturate; outline circular; exine tectate-perforate to semitectate-reticulate, 2.5–3.5 μm thick; tectum foveolate-fossulate or finely reticulate with perforations or lumina often irregular in size and shape, surface often uneven, microverrucate to densely and irregularly scabrate.

There is interspecific variation in the size of the perforations/lumina with *Tragia sellowiana* having a foveolate-fossulate tectum (Figs. 47, 48) and *T. lessertiana* having a reticulate tectum (Figs. 49, 50).

Tragia* sect. *Ctenomeria (Figs. 51–54). Section of two species of southern Africa. *Tragia capensis* examined here.

Pollen oblate-spheroidal (P/E = 0.89), 31 μm P × 35 μm E, with 3 poorly defined apertures; amb subcircular; aperture indistinct, appearing as an elliptic depressed area covered with a layer of exine distinctly thinner than the nonapertural exine, the apertural exine sometimes splitting in an irregular manner following acetolysis; exine tectate-perforate, ca. 2 μm thick, much thinner over the aperture; tectum very finely and irregularly foveolate-reticulate, lumina subcircular and often narrower than the muri, muri thick, uneven-surfaced, sometimes broken and incomplete, surface microspinulose; apertural sexine similar to but more irregular and finer than the nonapertural sexine, sometimes irregularly fragmented.

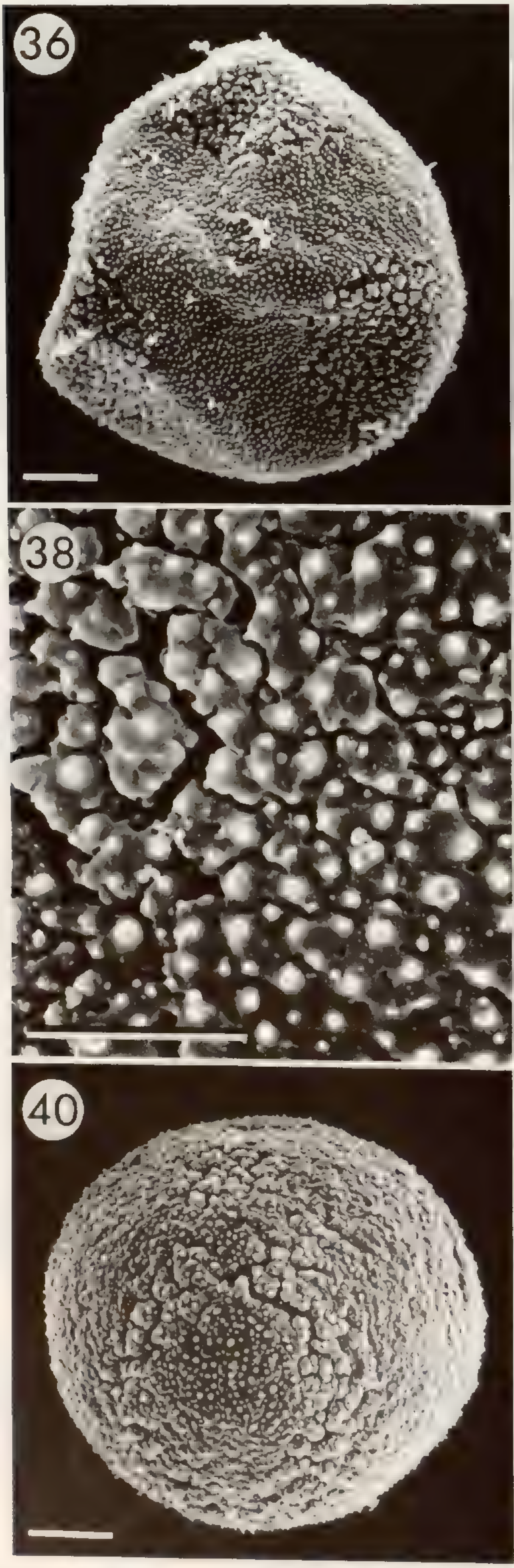
The foveolate-reticulate tectum is usually continuous over the aperture, with the aperture appearing as an elliptical depression under SEM and as a much thinner area of exine under LM. The apertures may be considered to be tenuitates, being indistinctly defined areas of thin exine (definition following Erdtman, 1952). Grains may have apertures folded inward in a direction parallel to the polar axis (Fig. 51). Following acetolysis many grains had apertures split in an irregular manner (Fig. 54).

Tragia* sect. *Lassia (Figs. 59, 60). Monotypic section of Madagascar consisting of *T. scandens*.

Pollen suboblate (P/E = 0.86), 33 P × 38.5 E, tricolpate; amb subcircular; colpus of narrow to medium width often with scattered, irregularly shaped islands of sexine, margin very uneven and indistinct; exine semitectate-reticulate, ca. 1.5 μm thick, uniformly thickened, fragmented at colpus margin; muri microverrucate to obscurely crenate; apertural sexine islands identical in sculpture to nonapertural sexine.

Tragia* sect. *Leptobotrys (Figs. 55–58). The section consists of two species of the southeastern United States; both species, *T. urens* and *T. smallii*, were examined.

Pollen oblate-spheroidal (P/E = 0.89–0.92), 34–37.5 μm P × 38–40.5 μm E, weakly triporate; amb subcircular to obtuse-triangular, angulaperturate; aperture circular to very broadly elliptic with margin indistinct, covered with a fragmented exine slightly thinner than the nonapertural exine, often split in an irregular manner; exine tectate-



FIGURES 36–41.[3] Scanning electron micrographs of pollen of *Cnesmone* and *Megistostigma* (subtribe Tragiinae). 36–38. *Cnesmone anisosepala*.—36. Polar view.—37. Atypical irregularly aperturate grain; note that the fragmented apertural sexine does not form three apertures.—38. Close-up of aperture margin with fragmented apertural sexine

perforate, 1–1.5 μm thick, uniformly thickened; tectum punctate, with irregularly shaped raised areas, surface sparsely to densely microverrucate, microverrucae variable in size; apertural sexine consisting of small baculate, rounded, or conical islands, surface smooth or microverrucate.

The apertural sexine may be either continuous across the aperture (Figs. 55, aperture at top, 57) or split in an irregular manner with the underlying membrane protruding through the resulting hole(s) (Figs. 55, aperture at right, 56, 58).

Tragia sect. ***Tagira*** (Figs. 61–63). Section of ca. 60 species, primarily in dry areas of Africa but also found in southwest Asia. Four species examined here, *T. adenanthera*, *T. cordifolia*, *T. hispida*, and *T. involucrata*.

Pollen suboblate to oblate-spheroidal (P/E = 0.87–0.88), 31.5–38 μm P × 36–43.5 μm E, tricolpate; amb subcircular to obscurely obtuse-triangular; colpus of narrow to medium width, often with scattered, irregularly shaped islands of sexine, margin very uneven and indistinct; exine semitectate-reticulate, 1.5–3 μm thick, usually uniformly thickened throughout, fragmented at colpus margin; muri crenate or microverrucate, often with microprojections in 1 or 2 rows; apertural sexine islands identical in sculpture to nonapertural sexine.

Tragia sect. ***Tragia*** (Figs. 64–66). A New World section of ca. 55 species of herbs, shrubs, and twining vines, particularly abundant in dry subtropical areas. Eight species were examined here: *T. chlorocaulon*, *T. mexicana*, *T. pacifica*, *T. peltata*, *T. polyandra*, *T. ramosa*, *T. tristis*, and *T. volubilis*.

Pollen suboblate (P/E = 0.83–0.88), 25–37 μm P × 30–43.5 μm E, tricolpate; amb obtuse-triangular, sometimes obscurely so, angulaperturate; colpus usually broad, often with 1 to several widely scattered, irregularly shaped and sized islands of sexine, margin very uneven; exine intectate?-baculate or clavate, 1.5 3 μm thick; baculae or clavae usually freestanding, but sometimes closely abutting and appearing coalesced, apex often flat, with (1–)2–4(–5) microverrucae; apertural sexine similar in sculpture to the nonapertural sexine.

The exine is generally relatively thin (1.5–2 μm) and of uniform thickness throughout, but may sometimes be thicker (ca. 2.5 μm) at mid mesocolpium and thinner toward the aperture margins (e.g., *T. pacifica*).

Tragia sect. ***Zuckertia*** (Figs. 67–69). Monotypic section comprising *T. bailloniana* of Mesoamerica.

Pollen oblate-spheroidal (P/E = 0.90), 56 μm P × 62.5 μm E, tricolpate; amb obtuse-triangular, sometimes obscurely so, angulaperturate; colpus broad with margins uneven and jagged; exine semitectate-reticulate, ca. 2 μm thick, becoming thinner toward colpus margin; tectum finely reticulate, becoming finer near aperture margin, muri scabrate.

Section unknown: *Tragia novae-hollandiae* (Figs. 70, 71). A twining vine endemic to Australia and the only species of *Tragia* represented there.

Pollen oblate-spheroidal to suboblate (P/E = 0.88), 36 μm P × 41 μm E, with three poorly defined apertures; amb obtuse-triangular, angulaperturate; aperture circular to broadly elliptic, L/W ca. 1–1.5, with margin indistinct, covered with a fragmented exine slightly thinner than the nonapertural exine; exine tectate-perforate, ca. 1.5 μm thick, uniformly thickened; tectum punctate, with irregularly shaped raised areas, surface microverrucate; apertural sexine consisting of small, often conical or baculate islands, surface microverrucate.

Tragia subg. ***Mauroya*** (Figs. 72–74). Monotypic subgenus consisting of *T. ivohibeensis*, endemic to Madagascar.

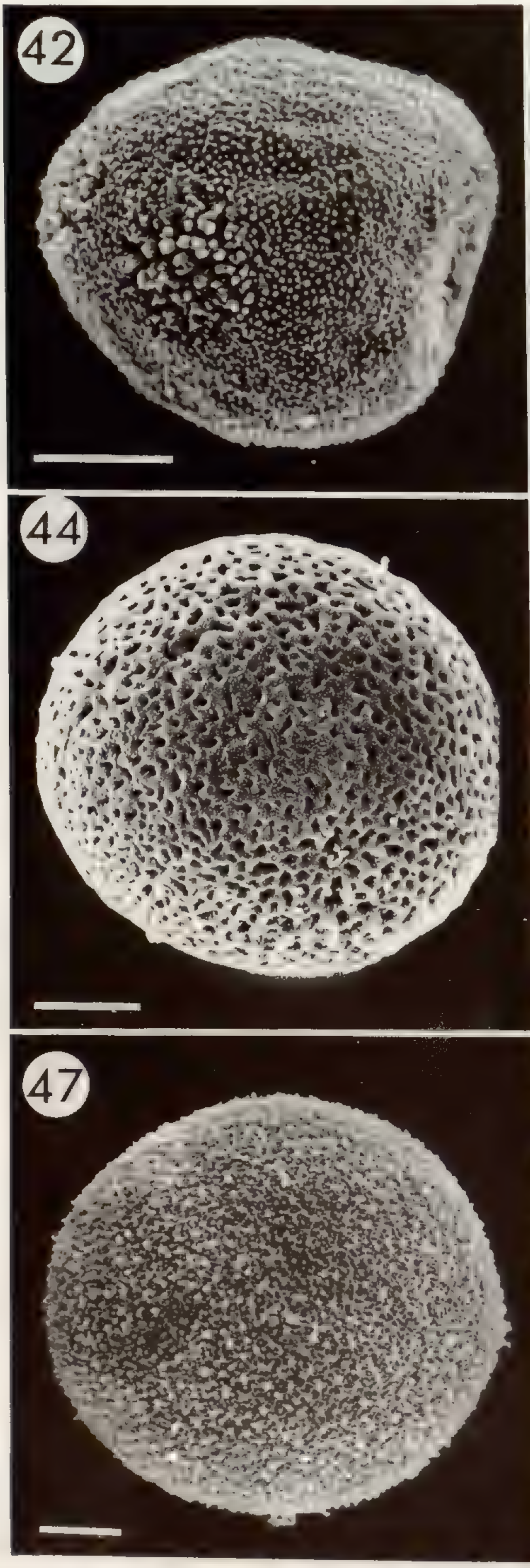
Pollen oblate-spheroidal (P/E = 0.91), 43.5 μm P × 48 μm E, with 3(–4) poorly defined apertures; amb circular to obscurely obtuse-triangular, angulaperturate; aperture indistinct, partially covered with fragments and strands of sexine, margin very indistinct; exine semitectate-reticulate, 1–1.5 μm thick, mostly uniformly thickened; tectum finely reticulate, muri microverrucate or microspinulose; apertural sexine fragments and strands similar in sculpture to the nonapertural sexine.

The poorly defined apertures appear to be irregular in size and shape, and are often difficult to discern in LM.

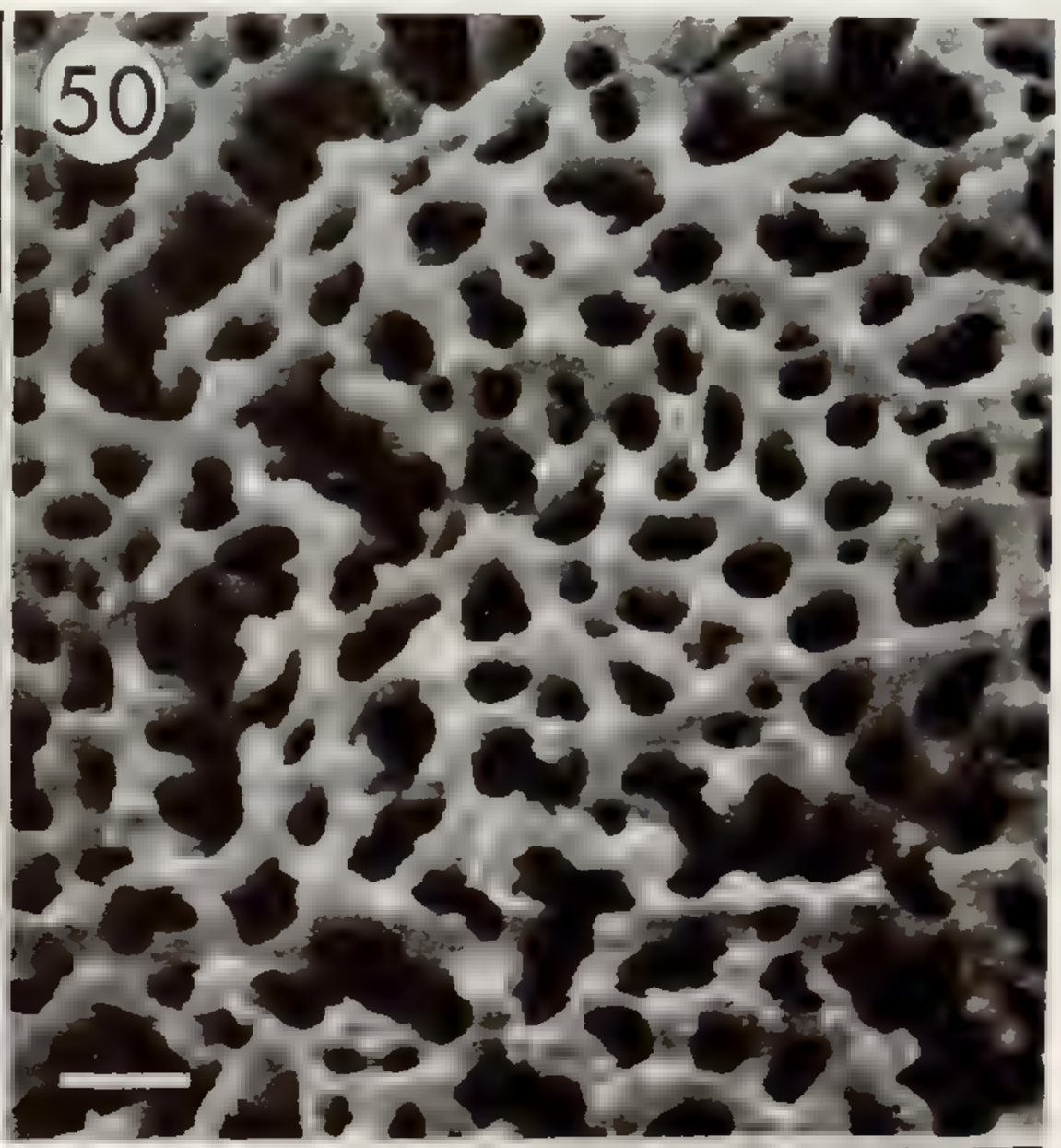
Tragiella (Figs. 75–77). Four species of twining or erect perennial herbs found in southern and eastern Africa. One species examined.

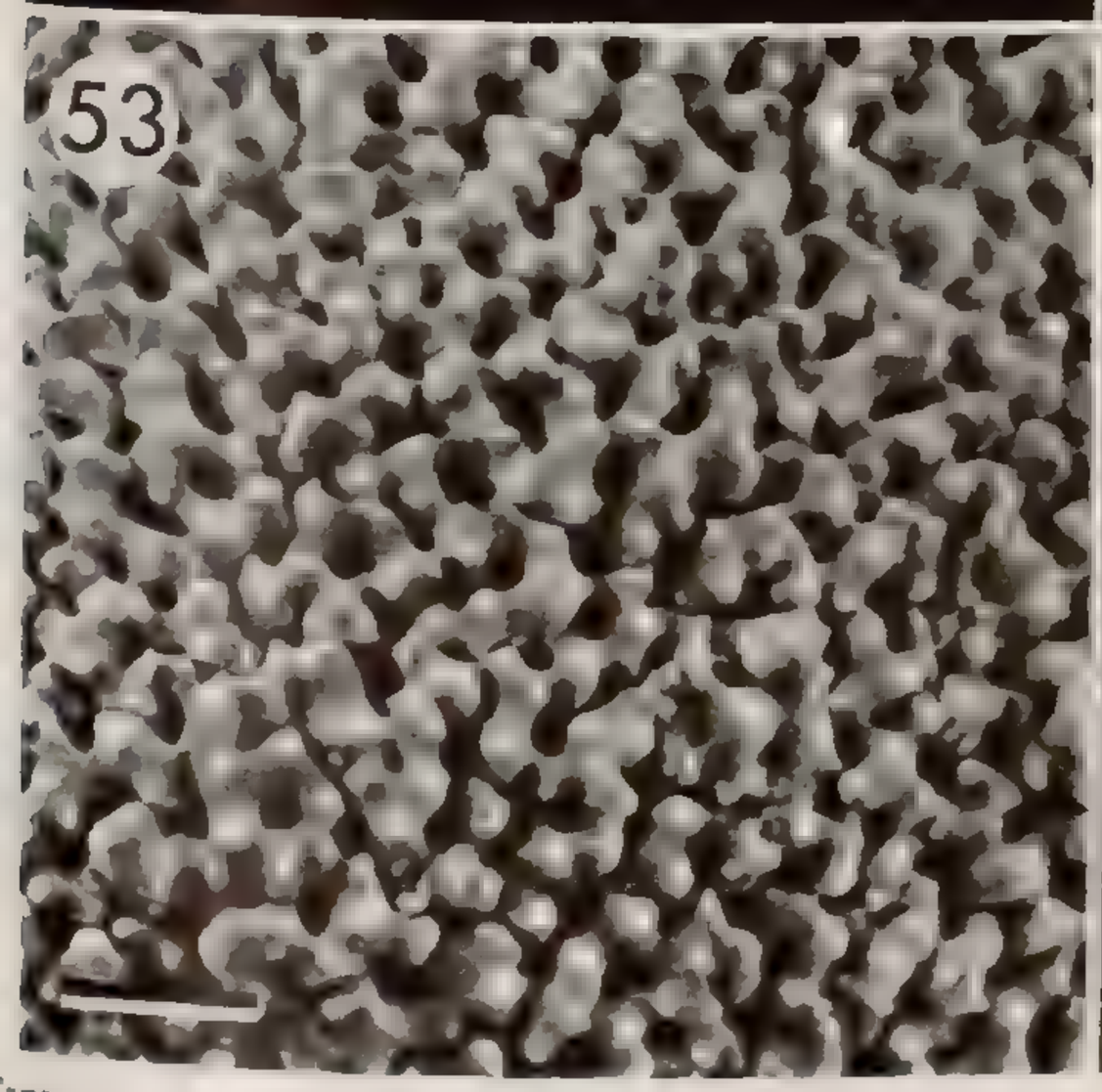
←

at left and nonapertural sexine at right.—39. Equatorial view of *Cnesmone tonkinensis*. 40–41. *Megistostigma malaccense* (Rahmat si Toroes 1389 A).—40. Irregularly aperturate grain.—41. Close-up showing nonapertural sexine surrounded by fragmented apertural sexine. Scale bar: = 10 μm in Figs. 36, 37, 39, 40; = 5 μm in Figs. 38, 41.

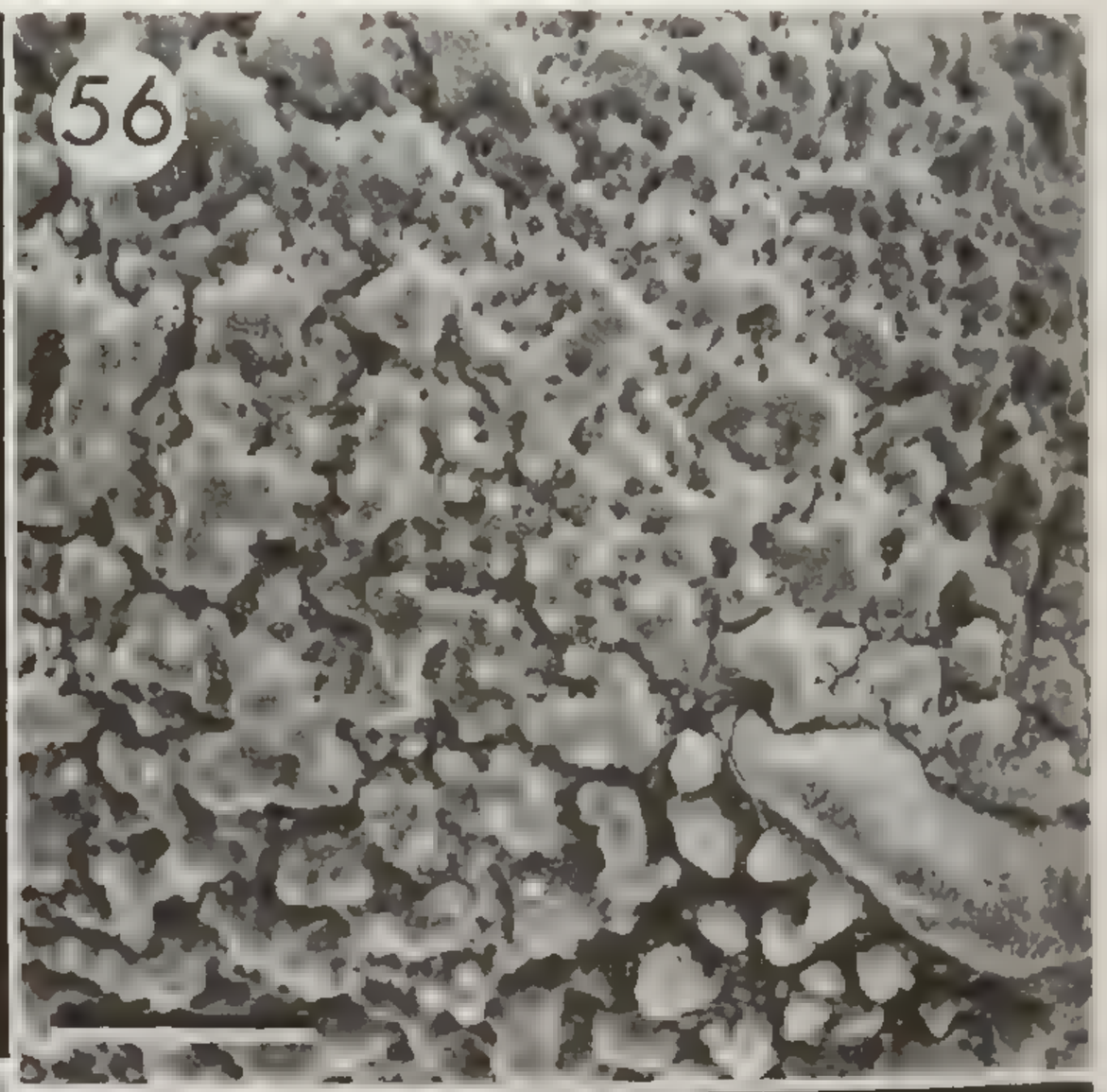


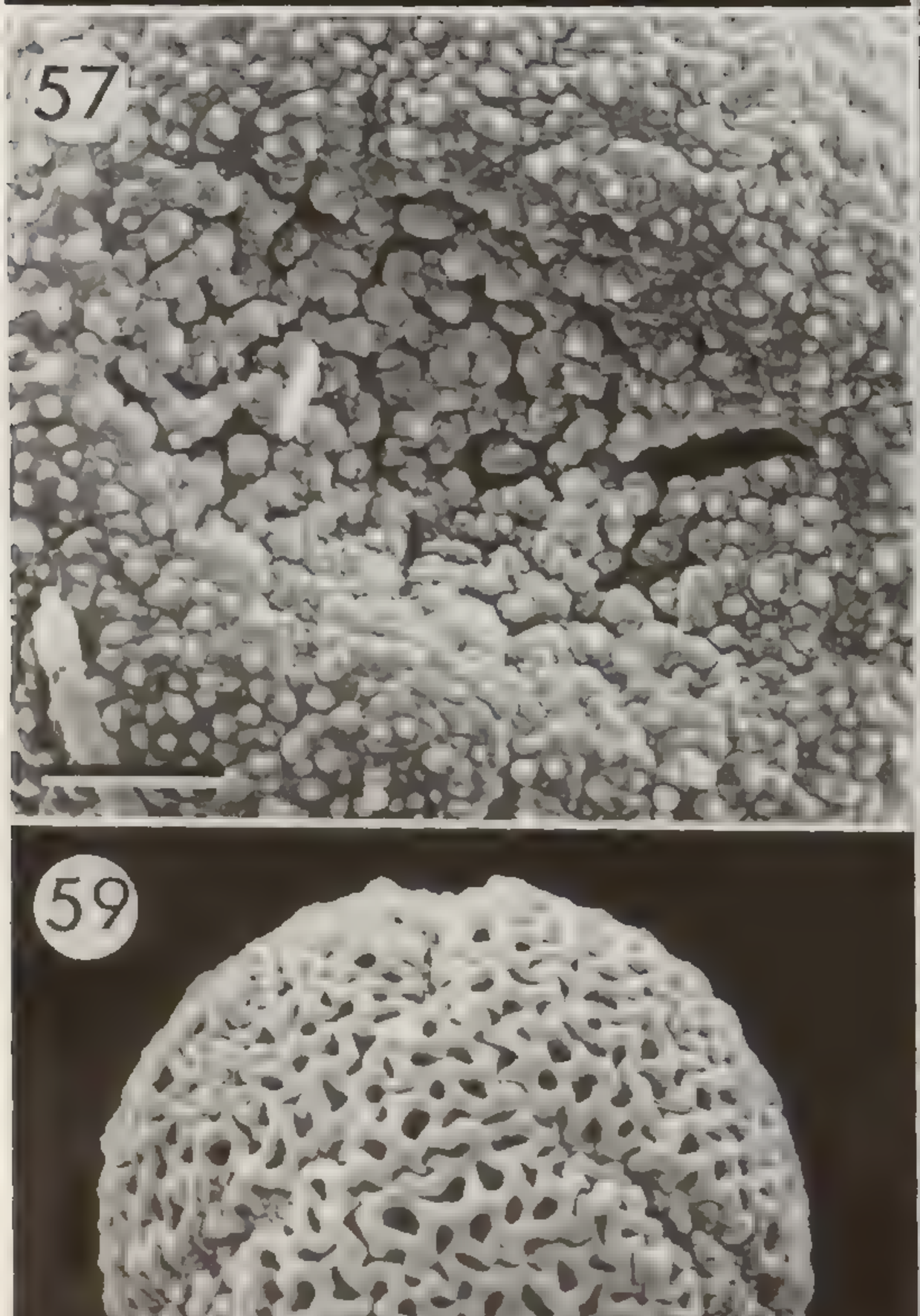
FIGURES 42–48. Scanning electron micrographs of pollen of *Pachystylidium*, *Platygyna*, and *Tragia* sect. *Bia* (subtribe Tragiinae). 42–43. *Pachystylidium hirsutum* (Ramos & Edaño 49201 UC).—42. Equatorial view showing circular apertures, with aperture at right visible as depressed area. 43. Close-up showing aperture covered with islands of sexine at bottom center surrounded by nonapertural exine.—44. Grain of *Platygyna hexandra*.—45. Exine sculpture of *Platygyna leonis*.—46. Exine sculpture of *Platygyna parvifolia*. 47–48. *Tragia* sect. *Bia*: *T. sellowiana*.—47. Whole grain.—48. Exine sculpture. Scale bar: = 10 μm in Figs. 42, 44, 47; = 2 μm in Figs. 43, 45, 46, 48.

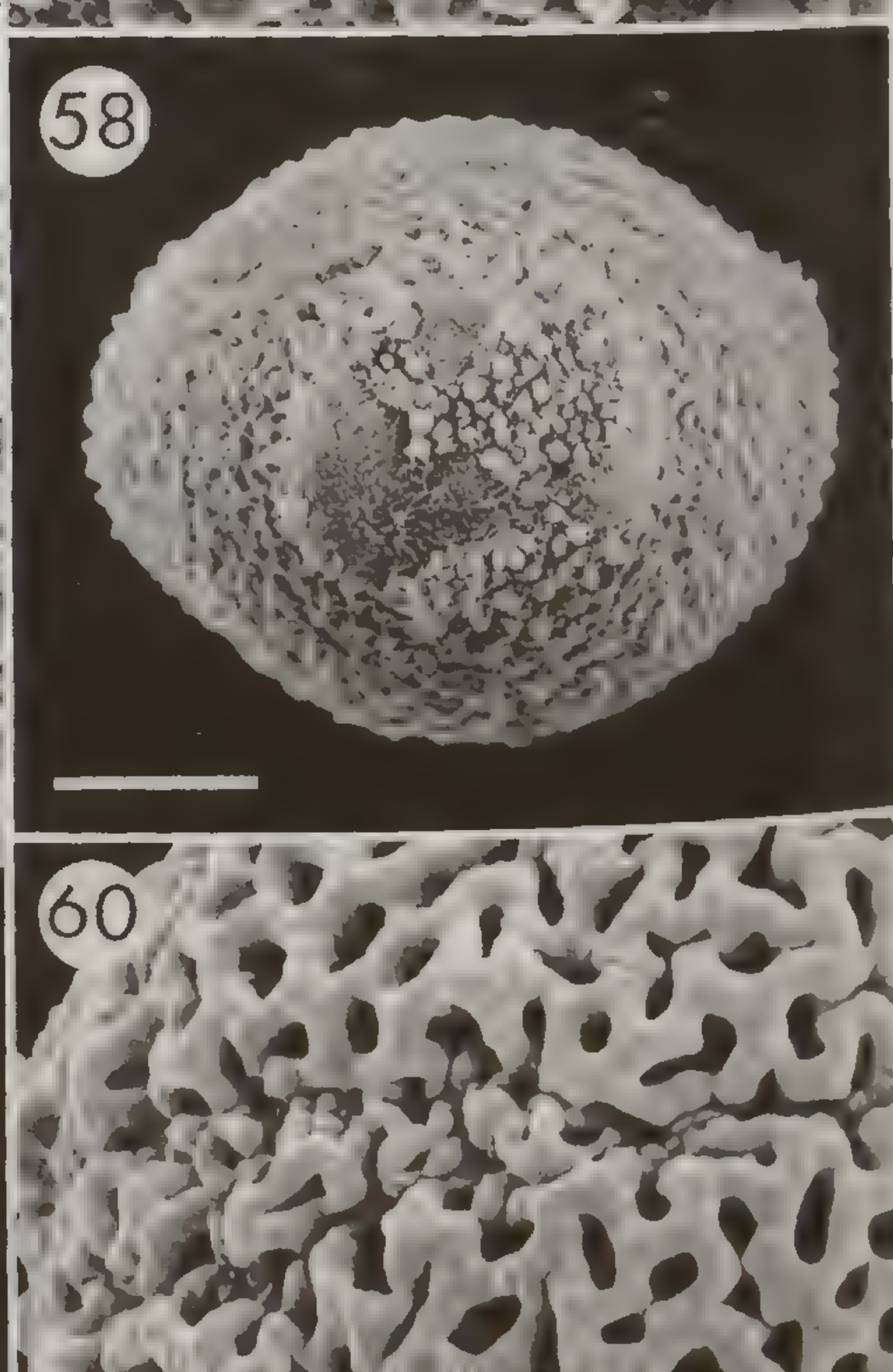




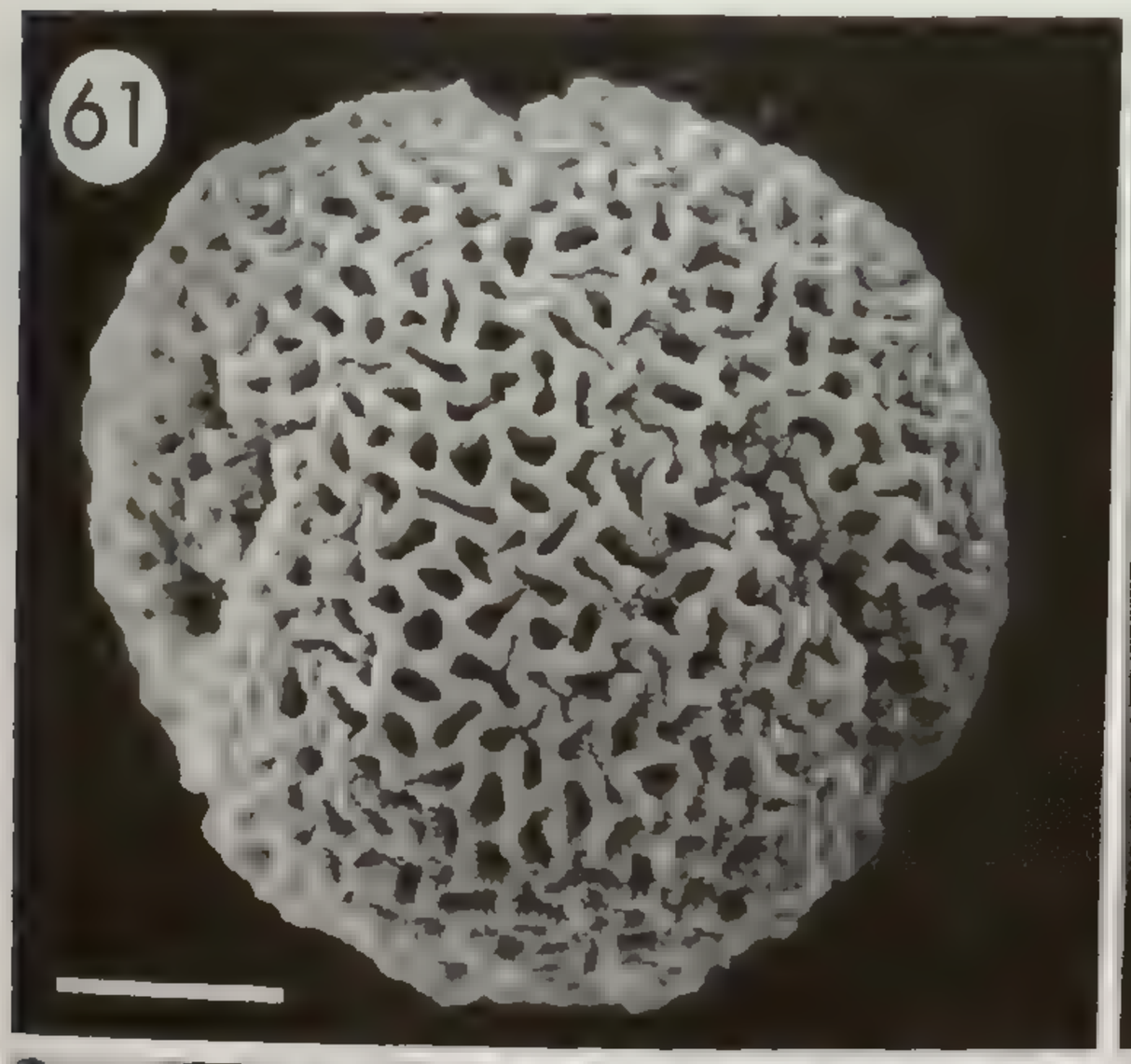
FIGURES 49–54.[3] Scanning electron micrographs of pollen of *Tragia* sect. *Bia* and *Tragia* sect. *Ctenomeria*. 49–50. *Tragia* sect. *Bia*: *T. lessertiana*.—49. Whole grain.—50. Exine sculpture. 51–54. *Tragia* sect. *Ctenomeria*: *T. capensis* (Kuntze s.n. NY). 51. Equatorial view.—52. Oblique view.—53. Exine sculpture.—54. Equatorial view of acetolyzed grain with ruptured apertural exine. Scale bar: = 10 μm in Figs. 49, 51, 52, 54; = 2 μm in Figs. 50, 53.

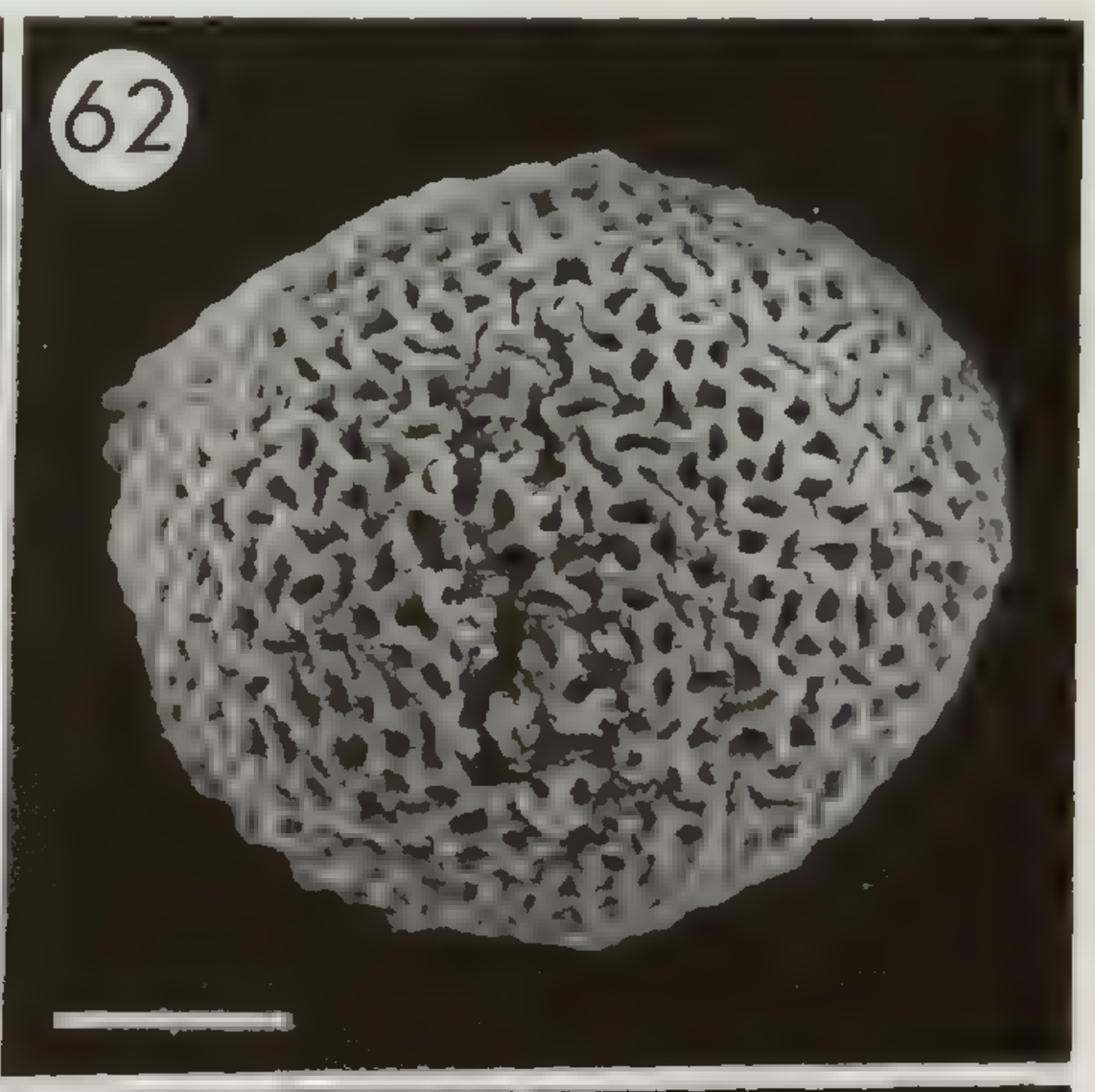


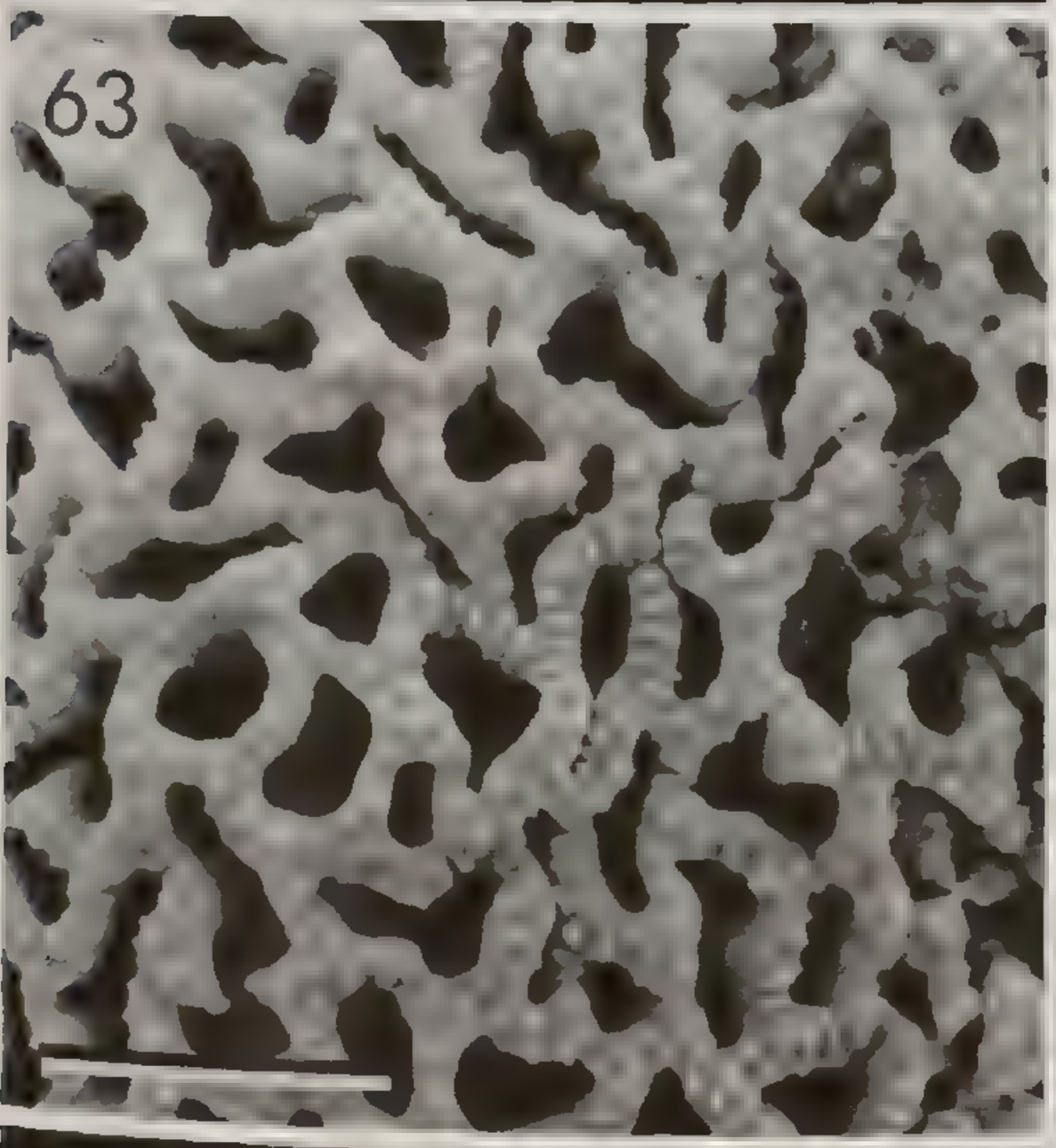


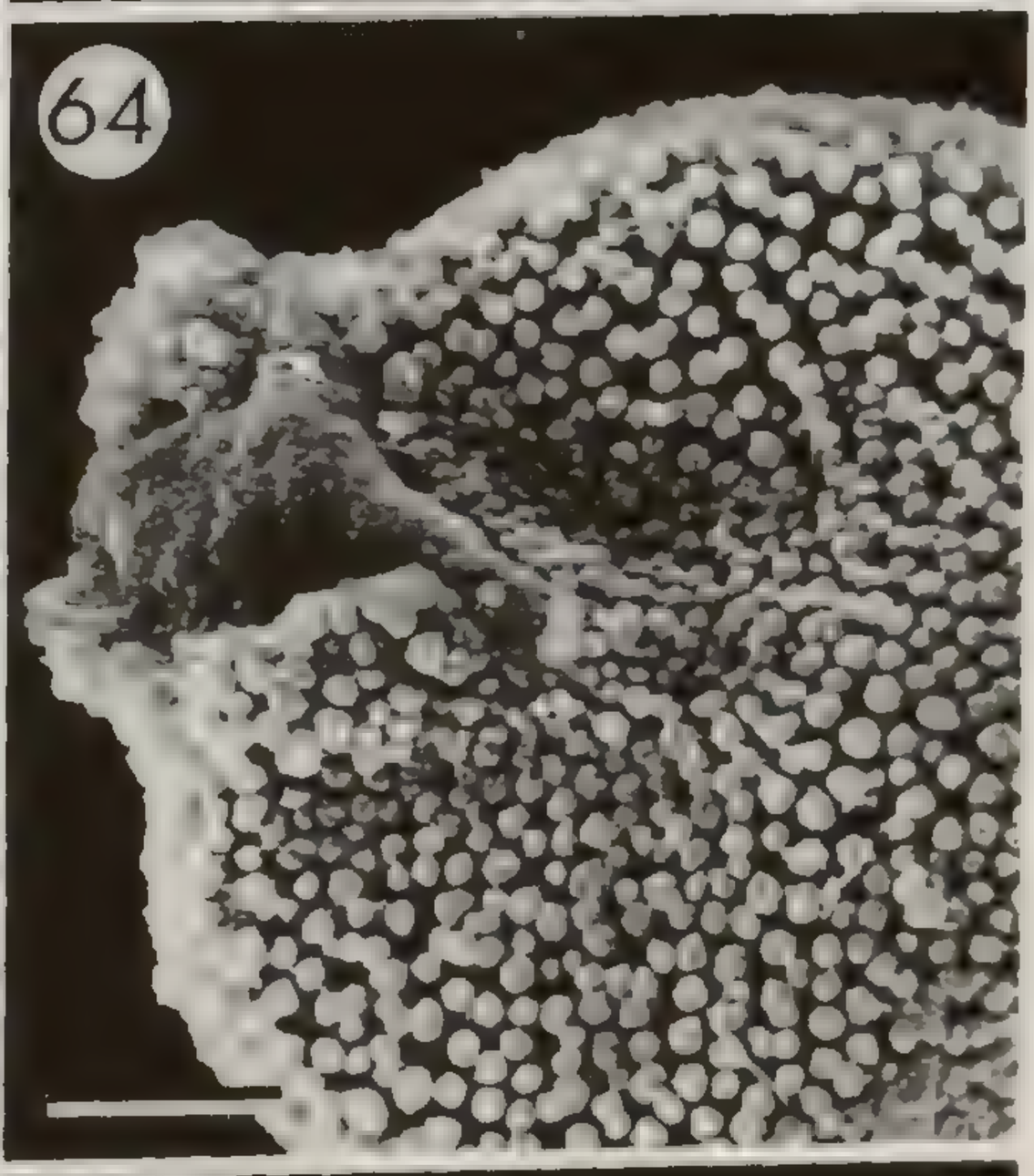


FIGURES 55–60.[3] Scanning electron micrographs of pollen of *Tragia* sect. *Leptobotrys* and *Tragia* sect. *Lassia*. 55–58. *Tragia* sect. *Leptobotrys*. 55, 56, 58. *T. urens*. —55. Polar view; note aperture at lower right with a split apertural sexine. —56. Close-up of aperture with split apertural sexine at lower right and nonapertural exine at upper left. —57. Close-up of *T. smallii* showing depressed circular aperture. —58. Equatorial view of *T. urens* showing circular aperture with ruptured apertural sexine. 59–60. *Tragia* sect. *Lassia*: *T. scandens*. —59. Oblique view. —60. Close-up of colpus and exine sculpture. Scale bar: = 10 μm in Figs. 55, 58, 59; = 5 μm in Figs. 56, 57, 60.

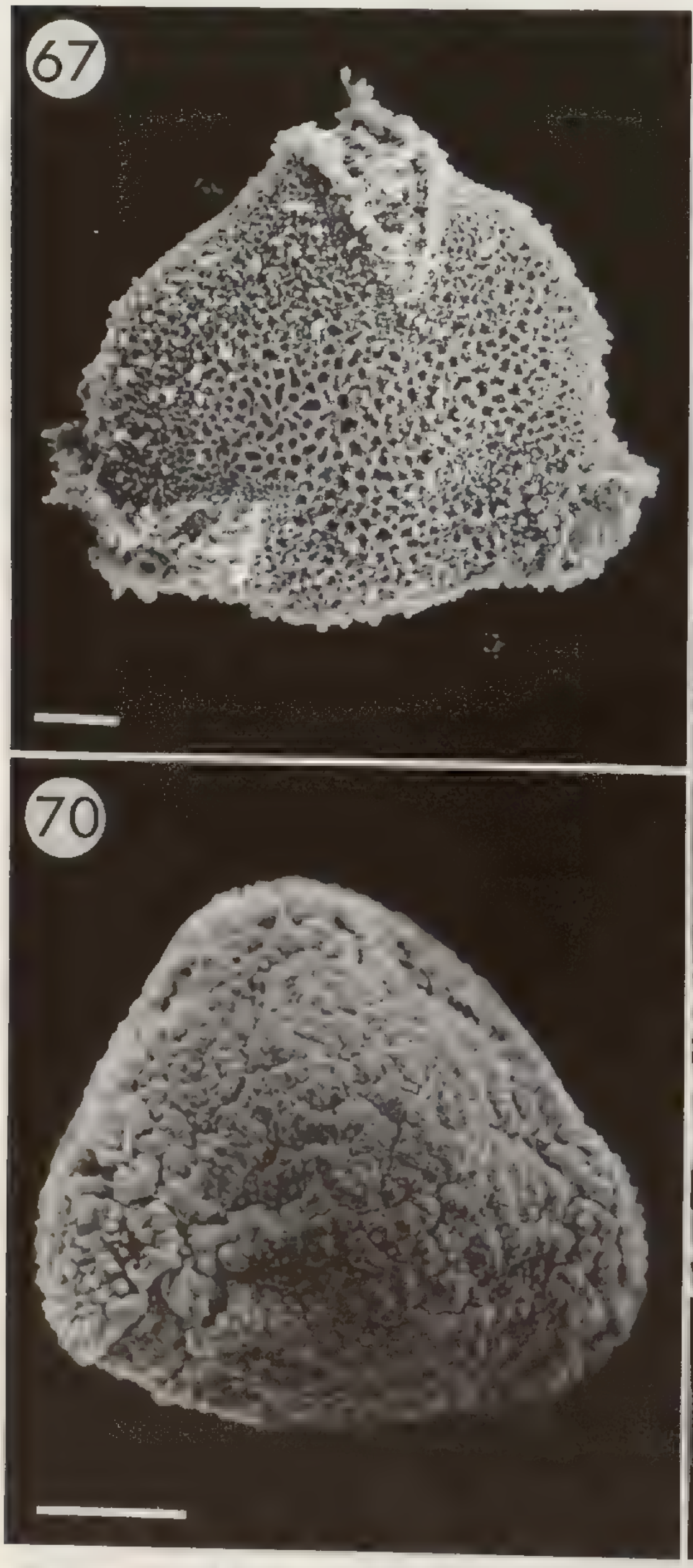


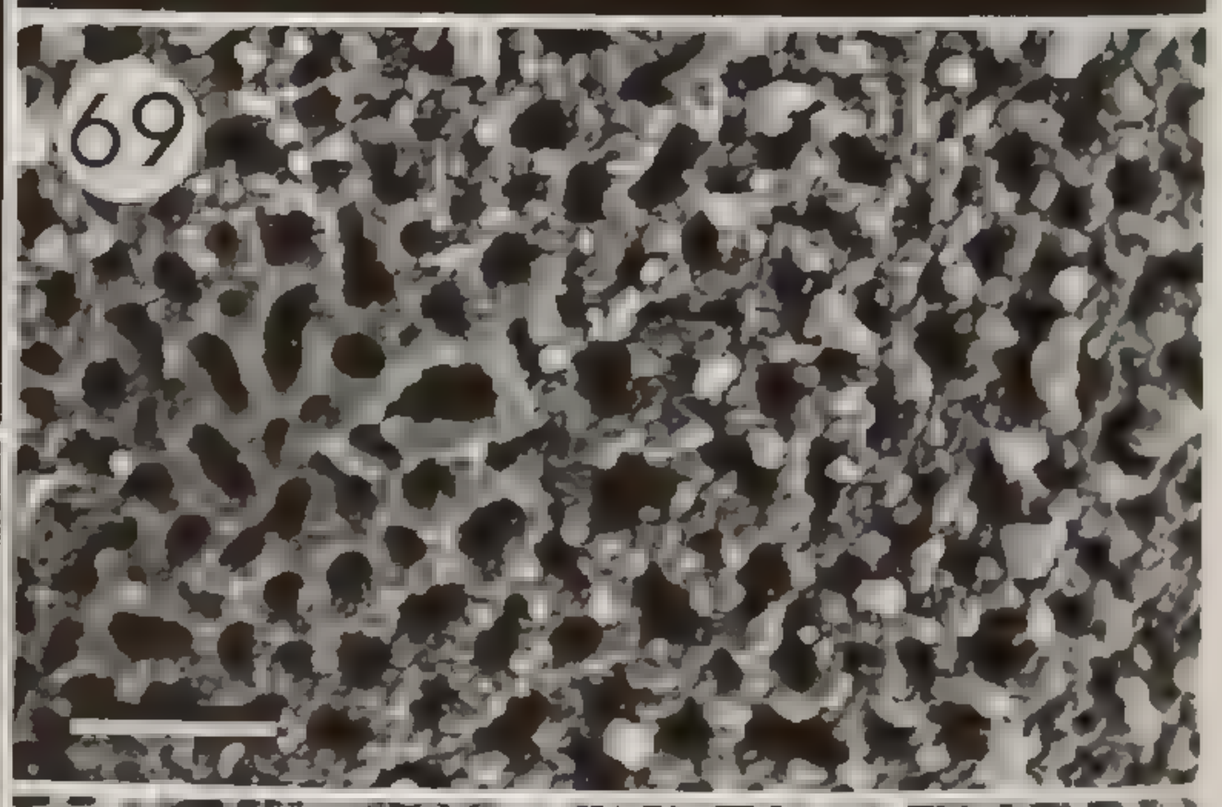


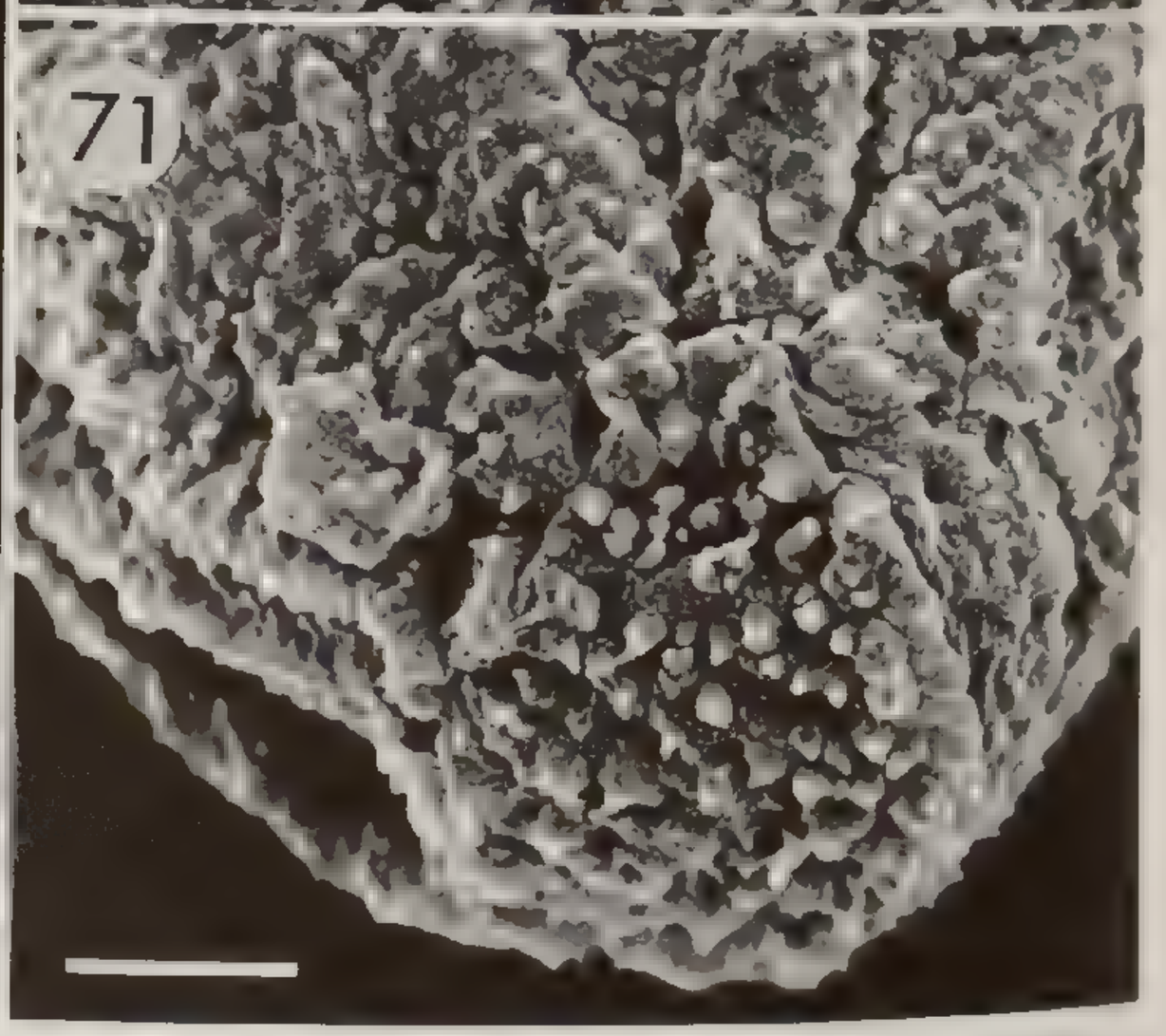




FIGURES 61–66. Scanning electron micrographs of pollen of *Tragia* sect. *Tagira* and *Tragia* sect. *Tragia*. 61–63. *Tragia* sect. *Tagira*: *T. adenanthera*.—61. Oblique view.—62. Equatorial view. 63. Exine sculpture with uneven and indistinct colpus margin at right. 64–66. *Tragia* sect. *Tragia*. 64. Close-up of colpus in polar view of *T. ramosa*. 65. Polar view of *T. volubilis*. –66. Equatorial view of *T. volubilis* showing colpus with scattered sexine islands. Scale bar: = 10 μm in Figs. 61, 62, 65, 66; = 5 μm in Figs. 63, 64.







FIGURES 67–71. Scanning electron micrographs of pollen of *Tragia* sect. *Zuckertia* and *Tragia novae-hollandiae*. 67–69. *Tragia* sect. *Zuckertia*: *T. baillouana*. —67. Polar view. —68. Equatorial view. —69. Exine sculpture. 70–71. *T. novae-hollandiae*. —70. Polar view. —71. Close-up of circular aperture and exine sculpture. Scale bar: = 10 μm in Figs. 67, 68, 70; = 5 μm in Figs. 69, 71.

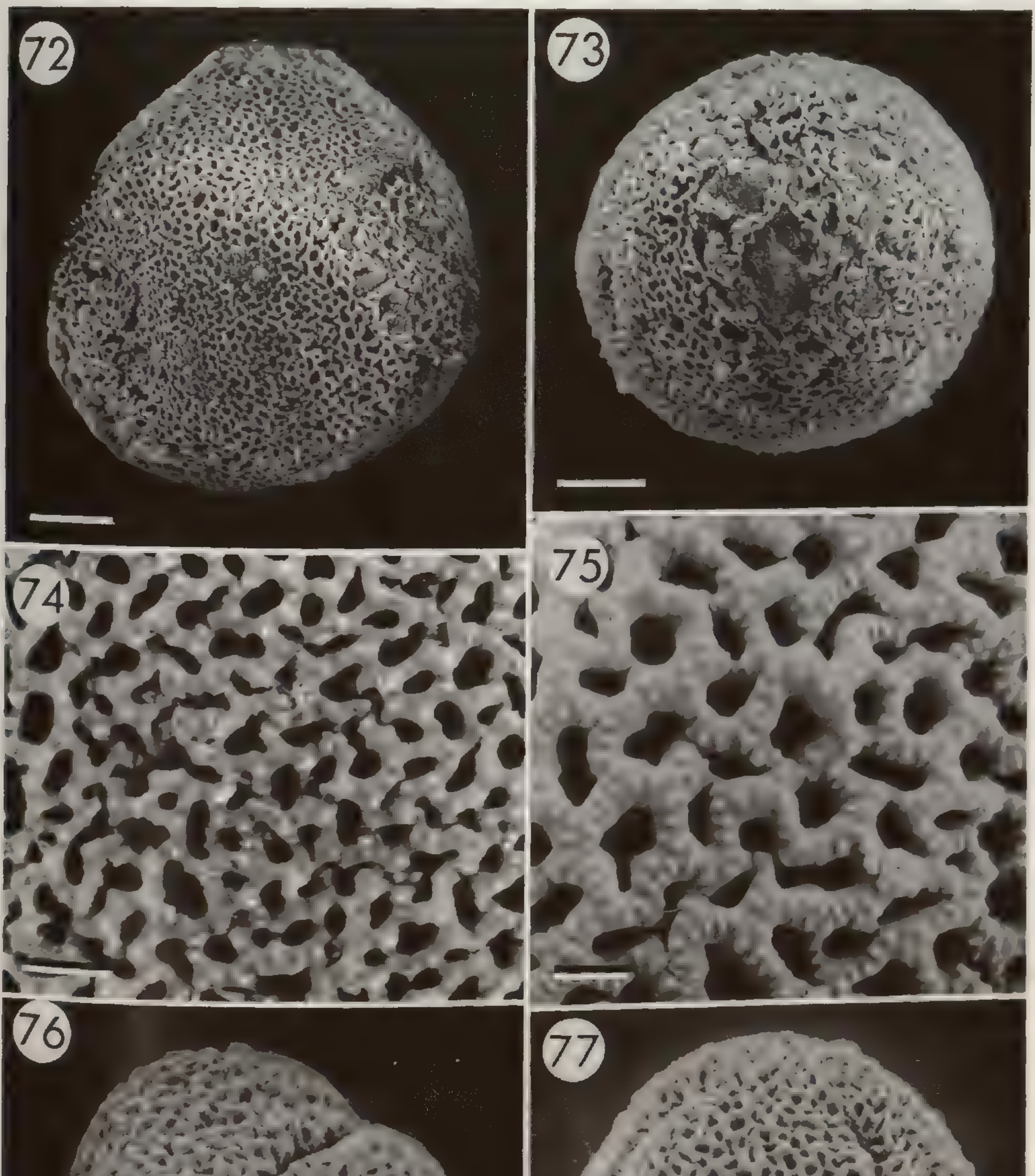
Pollen oblate-spheroidal (P/E = 0.91), 42.5 μm P × 46.5 μm E, tricolpate; amb subcircular; colpus narrow, margin very uneven; exine semitectate-reticulate, ca. 2.5 μm thick, mostly uniformly thickened; muri microverrucate or sometimes appearing crenate with transversely oblong microverrucae.

No evidence of apertural sexine islands was seen under LM or in acetolyzed pollen in SEM.

DISCUSSION

GENERAL POLLEN MORPHOLOGY OF THE PLUKENETIEAE AND PHYLOGENETIC IMPLICATIONS

A diversity of pollen morphology was found in the Plukenetieae, including tricolpate, weakly aperturate, and inaperturate pollen with exine structure ranging from tectate, semitectate, to apparently intectate (Table 2). Apertures, when present, are



FIGURES 72–77. Scanning electron micrographs of pollen of *Tragia* subgenus *Mauroya* and *Tragiella* (subtribe Tragiinae). 72–74. *Tragia* subgenus *Mauroya*: *T. ivohibeensis*.—72. Polar view.—73. Equatorial view showing poorly defined aperture covered with strands and fragments of sexine.—74. Exine sculpture. 75–77. *Tragiella natalensis*, acetolyzed grains.—75. Exine sculpture.—76. Polar view.—77. Equatorial view. Scale bar: = 10 μm in Figs. 72, 73, 76, 77; = 2 μm in Figs. 74, 75.

TABLE 2. Pollen morphology of the Plukenetieae. Aperture condition, tectum morphology (i.e., nonapertural), and presence and distribution of apertural sexine is outlined for each genus, including each section of *Tragia* and each pollen type (if more than one). The category "absent" also includes the condition of very small fragments of sexine that do not form distinct islands on the apertural membrane.

Genus	Aperture condition	Tectum morphology	Apertural sexine	Figures
Plukenetiinae				
Angostyles	tricolpate	finely foveolate-rugulate	absent	1–3
Astrococcus	tricolpate	finely foveolate-rugulate	absent—or present and continuous	4–6
Eleutherostigma	tricolpate	foveolate	absent	7–8
Haematostemon	tricolpate	finely foveolate-rugulate	absent—or present and continuous	9–13
Plukenetia Type 1	tricolpate	foveolate	absent	14–19
Type 2	tricolpate	reticulate	absent	20–24
Romanoa	tricolpate	fossulate-foveolate	absent	25–27
Vigia	tricolpate	reticulate	absent	28–29
Tragiinae				
Acidoton Type 1	tricolpate	finely & irregularly foveolate-reticulate	scattered islands	30–32
Type 2	inaperturate	rugulate	—	33–35
Cnesmone	weakly tricolpate	punctate	dense covering of small islands	36–39
Megistostigma	weakly tricolpate, irregularly aperturate or inaperturate	punctate	dense covering of small islands	40–41
Pachystylidium	weakly triporate	punctate	dense covering of small islands	42–43
Platygyna	inaperturate	reticulate or rugulate	—	44–46
Tragia sect. *Bia*	inaperturate	foveolate-fossulate or finely reticulate	—	47–50
T. sect. *Ctenomeria*	weakly 3-aperturate	finely & irregularly foveolate-reticulate	continuous but thinner, sometimes fragmented	51–54
T. sect. *Lassia*	tricolpate	reticulate	scattered islands	59–60
T. sect. *Leptobotrys*	weakly triporate	punctate, uneven-surfaced	dense covering of small islands	55–58
T. sect. *Tagira*	tricolpate	reticulate	scattered islands	61–63
T. sect. *Tragia*	tricolpate	baculate	few scattered islands	64–66
T. sect. *Zuckertiana*	tricolpate	finely reticulate	absent	67–69
T. novae-hollandiae	weakly triporate	punctate, uneven-surfaced	dense covering of small islands	70–71
T. subg. *Mauroya*	weakly 3-aperturate	finely reticulate	irregularly fragmented into strands	72 74
Tragiella	tricolpate	reticulate	absent?	75–77

simple, i.e., they lack differentiated endoapertures or ora. An unusual feature is the presence of several different types of weakly defined apertures. Invariant character states include medium to large size and suboblate to spheroidal shape (i.e., with the polar axis shorter than or equal to the equatorial axis).

The majority of Euphorbiaceae have tricolporate pollen; their compound apertures consist of an outer colpus and an inner os. Colpate, porate, and inaperturate conditions are uncommon in the family outside of the Plukenetieae except within the two subfamilies Oldfieldioideae and Crotonoideae. The Oldfieldioideae are characterized by brevicolporate or porate echinate pollen (Levin & Simpson, 1994). The Crotonoideae are characterized by the presence of a crotonoid exine structure (Nowicke, 1994), with the inaperturate condition most common and the colpate and porate aperture conditions characteristic of taxa considered by Webster (1994) to be least derived within the subfamily. Both subfamilies appear to be distantly related to the Plukenetieae on the basis of floral, vegetative, and pollen exine characters. Inaperturate pollen is not found elsewhere in the Euphorbiaceae and porate pollen is found rarely and only in distantly related phyllanthoid taxa (e.g., *Phyllanthus* L., *Hymenocardia* Wall. ex Lindl.).

The Acalyphoideae are characterized primarily by tricolporate pollen; however, there are also occurrences of tricolpate pollen outside of the Plukenetieae. These include three of five genera in subtribe Ditaxinae of the Chrozophoreae (*Argythamnia* P. Browne, *Chiropetalum* A. Juss., *Ditaxis* Vahl) characterized by tricolpate operculate pollen, subtribe Cephalomappinae of the Epiprineae (*Cephalomappa* Baill.) characterized by brevicolpate pollen, and tribe Omphaleae (*Omphalea*) having pollen resembling but distinct from *Plukenetia* (Punt, 1962; Gillespie, 1988; pers. obs.). Both the tricolpate and tricolporate aperture conditions have been described for pollen of *Adelia* L., *Lasiocroton* Griseb., *Leucocroton* Griseb. (all in tribe Adelieae), and *Erismanthus* Wall. ex Muell. Arg. (tribe Erismantheae) (Erdtman, 1952; Punt, 1962; pers. obs.). Subtribe Dysopsidinae of the Acalypheae (*Dysopsis* Baill.) has pollen with three weakly defined apertures superficially similar to but structurally different from *Tragia capensis* (Fernández-González et al., 1994; Suárez-Cervera, pers. comm.). Therefore, based on comparison with the remainder of the Acalyphoideae the tricolpate condition would appear to be most primitive in the Plukenetieae. Given that the most plausible direction of evolution of aperture condition in the tribe is tricolporate → tricolpate → weakly tricolpate, triporate or 3-aperturate → inaperturate (Fig. 78), the tricolpate condition would still be considered most primitive in the Plukenetieae even if it is not homologous with the same condition in other Acalyphoideae, but was separately derived from the tricolporate condition through loss of the endoaperture.

The genus *Dalechampia* was treated as a subtribe of the Plukenetieae by Webster (1994) in his most recent classification. However, the distinctive pollen of *Dalechampia* (Punt, 1962; Webster & Webster, 1972: fig. 25) is very different from any pollen type found within the Plukenetieae (as circumscribed here, i.e., sensu Webster, 1975). Pollen of *Dalechampia* is subspheroidal to prolate, tricolporate with thickened equatorial bands of exine, and coarsely reticulate. The tricolporate aperture condition of *Dalechampia* does not support the hypothesis that the genus was derived from within the Plukenetieae as suggested by Webster & Webster (1972), given that the independent evolution of an endoaperture is a much less likely event than its loss. If *Dalechampia* is instead the sister group of the Plukenetieae, their common ancestor would presumably have had tricolporate pollen. This would imply that the tricolpate condition is a synapomorphy defining the Plukenetieae and is not homologous with the tricolpate state of other members of the Acalyphoideae.

POLLEN MORPHOLOGY AND PHYLOGENETIC IMPLICATIONS IN SUBTRIBE PLUKENETIINAE

Subtribe Plukenetiinae is relatively uniform in pollen morphology, characterized by tricolpate pollen with well defined apertures having an uneven, sometimes jagged margin (Table 2). *Plukenetia* (Figs. 14–24) has pollen with broad colpi having very uneven, jagged margins, an amb that is obtuse-triangular and angulaperturate or less often subcircular, and a foveolate or reticulate tectum. Two pollen types may be distinguished based on tectum morphology (Table 2); these types correspond approximately to groups distinguished by Punt (1962), but are more narrowly defined and restricted to *Plukenetia* (i.e., foveolate Type 1 pollen with Punt's *Plukenetia volubilis* subtype and reticulate Type 2 pollen with the *Plukenetia verrucosa* subtype). Species having Type 1 pollen may be subdivided geographically into a neotropical group characterized by large grains with a thick exine that tapers toward the margin and a paleotropical group characterized by medium-sized grains having a thinner exine that is uniformly thick or

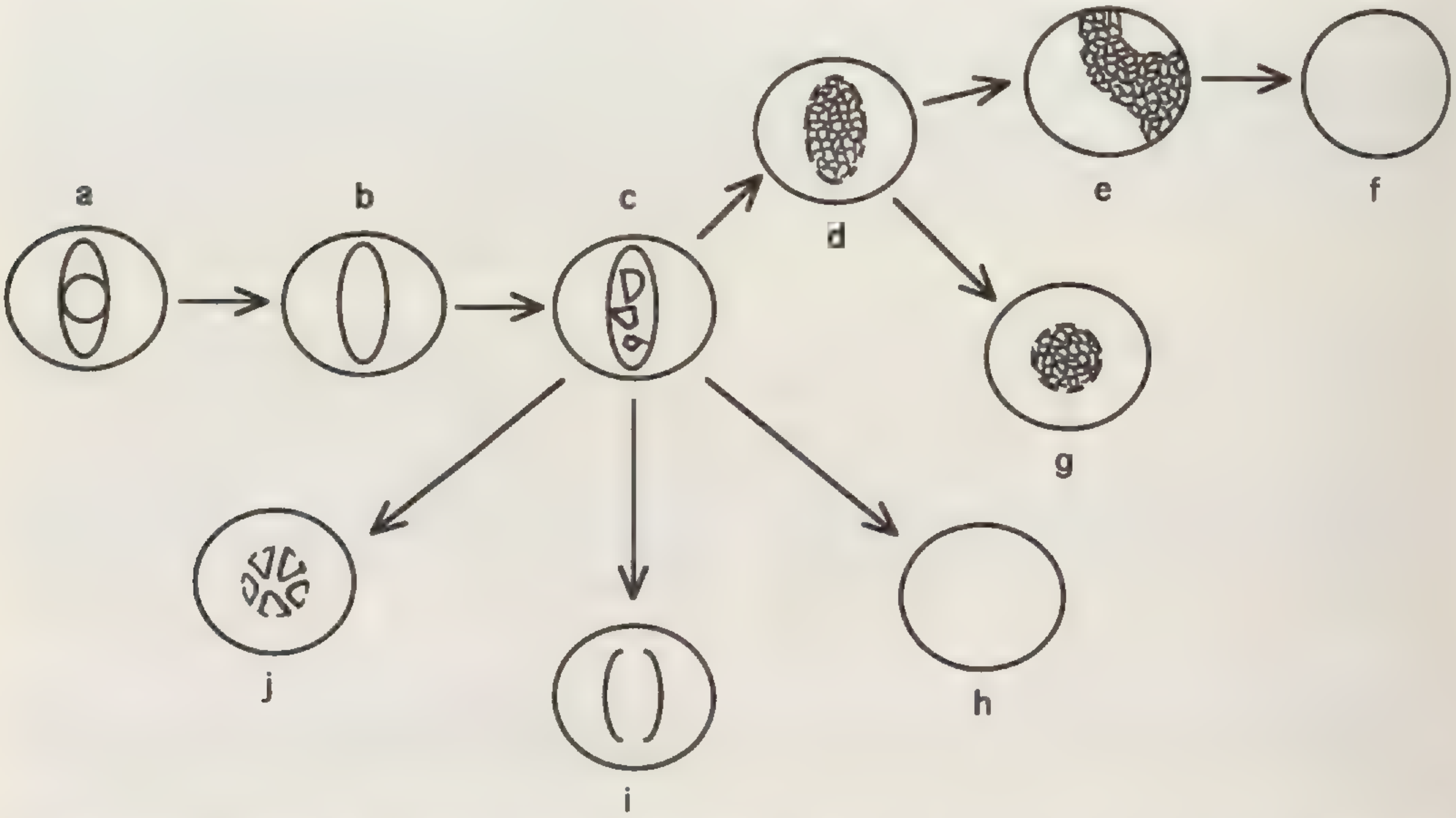


FIGURE 78. Evolution of aperture condition in the Plukenetieae: a hypothetical character state tree. Note that only one aperture is shown in equatorial view, and that only apertural condition is schematically illustrated, not details such as aperture margin morphology. a. Ancestral tricolporate condition (*Dalechampia*, most Acalyphoideae).—b. Tricolpate (all Plukenetiinae, *Tragia* sect. *Zuckertia*).—c. Tricolpate with scattered sexine islands on apertural membrane (*Tragia* sect. *Tragia*, *Tragia* sect. *Tagira*, *Acidoton* Type 1).—d. Weakly tricolpate, apertures with dense covering of small sexine islands (*Cnesmone*, *Megistostigma*).—e. Irregularly aperturate, apertural areas with a dense covering of small sexine islands (*Megistostigma*). —f. Inaperturate (*Megistostigma*).—g. Weakly triporate, apertures with dense covering of small sexine islands (*Pachystylidium*, *Tragia* sect. *Leptobotrys*, *Tragia novae-hollandieae*).—h. Inaperturate (*Acidoton* Type 2, *Platygyna*, *Tragia* sect. *Bia*).—i. Weakly 3-aperturate, apertural areas covered with thin layer of exine, usually visible as depressions (*Tragia* sect. *Ctenomeria*).—j. Weakly 3-aperturate, apertural areas covered with strands of sexine (*Tragia* subgenus *Mauroya*).

thicker at the aperture margin. Species having Type 2 pollen, known only from the Neotropics, may also be subdivided into two groups using the above criteria. The two pollen types and subgroups appear to have a phylogenetic basis and reflect current ideas of species relationships in the genus (Gillespie, 1993). Among neotropical species, pollen morphology, together with degree of style fusion and androecium morphology, may be used to define major species groups.

Pollen morphology of the monotypic genera *Eleutherostigma* (Figs. 7, 8) and *Vigia* (Figs. 28, 29) fits well within the range of variation found in *Plukenetia*, thus strongly supporting their recent synonymy under *Plukenetia* (Gillespie, 1993). *Eleutherostigma* has pollen of Type 1 and appears to be very closely related to the other neotropical species included in Type 1, while *Vigia* has pollen of Type 2 that is medium sized, similar to *P. verrucosa*, *P. penninervia*, and related species.

Romanoa (Figs. 25–27) also has pollen very similar to that of *Plukenetia*, but differs in its fossulate-foveolate tectum. Although morphologically very similar to *Plukenetia*, the genus may be distinguished by its trilocular ovary and 5-parted pistillate calyx, both plesiomorphic characters in the subtribe. *Romanoa tamnoides* appears to be either the sister taxon of *Plukenetia*, which is characterized by a 4-locular ovary and 4-parted calyx, or its most plesiomorphic member.

Angostyles (Figs. 1–3), *Astrococcus* (Figs. 4–6), and *Haematostemon* (Figs. 9–13) share a very similar pollen morphology, which is distinct in colpus and tectum morphology from that of the other genera of subtribe Plukenetiinae described above (Table 2). Pollen is subcircular and not distinctly triangular, with a very finely rugulate, microverrucate tectum. Colpi are narrower with an uneven but not distinctly jagged margin. The three genera share a trilocular ovary and a tree or shrub habit, very different from the vine or liana habit of *Plukenetia* and *Romanoa*. Both *Astrococcus* and *Haematostemon* have unusually thickened aperture margins with the upper and lower exine layers separating to form an elongate chamber (similar to a vestibulum). Pollen characters together with an androecium of four stamens, a unique character in the subtribe, suggest their very close relation-

ship. In contrast, *Angostyles* lacks the thickened aperture margin and elongate chamber and bears staminate flowers with numerous stamens. Thus while *Angostyles*, *Astrococcus*, and *Haematostemon* form a distinct group, the latter two are most closely related and *Angostyles* is the least derived member sharing with *Plukenetia* the plesiomorphic characters of numerous stamens and absence of an elongate chamber. Punt (1962) also remarked that pollen morphology of *Angostyles* is intermediate, sharing with *Astrococcus* and *Haematostemon* a "tectum perforatum" (as opposed to a "psilate" tectum as described for other species in the *Plukenetia volubilis* subtype), but apparently lacking a "margo" (defined as a prominent or depressed margin) as in *Plukenetia* (except *P. conophora*).

POLLEN MORPHOLOGY AND PHYLOGENETIC IMPLICATIONS IN SUBTRIBE TRAGIINAE

Subtribe Tragiinae exhibits much greater diversity in pollen morphology than subtribe Plukenetiinae. Pollen is tricolpate, inaperturate, or with poorly defined apertures. Exine sculpture includes punctate, foveolate, rugulate, reticulate, and baculate conditions (Table 2). *Pachystylidium* and *Platygyna* are characterized by unique pollen types; *Acidoton* includes two distinct pollen types. The large genus *Tragia* includes seven very distinct pollen types, each characteristic of one or more sections with each section having a uniform pollen morphology.

Pollen of the West Indian genus *Platygyna* (Figs. 44–46) is inaperturate with a reticulate or rugulate tectum. No evidence was seen of small circular endexine thickenings observed by Punt (1962) on acetolyzed grains of *P. hexandra*. The generic status of *Platygyna* has been questioned (Liogier, 1971; Borhidi et al., 1973); only two floral characters, a globose or convex staminate receptacle and thickened papillose styles, separate the genus from *Tragia*. Palynologically, *Platygyna* appears to be quite distinct from *Tragia* with the exception of the neotropical section *Bia* (Figs. 47–50), the only section characterized by inaperturate pollen. *Platygyna* differs from section *Bia* in its smaller pollen grains with a coarser exine sculpture. Differences in inflorescence architecture, presence of disc segments or a globose receptacle in the staminate flowers and style morphology between these two taxa would seem to preclude a close relationship, suggesting that the similarity in pollen morphology, particularly the inaperturate condition, is due to convergence.

The genus *Acidoton* was found to contain two distinct pollen types, differing in aperture presence and exine sculpture. The tricolpate grains of the mainland neotropical species, *A. nicaraguensis*, have colpi with uneven margins and apertural sexine islands (Figs. 30–32). The inaperturate pollen of the West Indian species (Figs. 33–35) appears more similar to pollen of its geographical neighbor *Platygyna* (Figs. 44–46), particularly to *P. parvifolia*, than to its mainland congener. Interestingly, *P. parvifolia* appears morphologically intermediate between the two genera, having an intermediate stamen number and a staminate receptacle that is glabrous like *Acidoton* but globose like *Platygyna*. This suggests that the mainland species is not the sister taxon of the West Indian species of *Acidoton*, and therefore should be treated as the distinct genus *Gitara* Pax & K. Hoffm. (as originally considered by Pax & Hoffmann, 1924). An alternative hypothesis would be the origin of the inaperturate condition from the tricolpate condition within *Acidoton*, and independently from the inaperturate condition in *Platygyna*; however, given their very similar pollen including tectum morphology, this hypothesis would seem less probable.

The three Indomalaysian genera of subtribe Tragiinae, *Cnesmone* (Figs. 36–39), *Megistostigma* (Figs. 40, 41), and *Pachystylidium* (Figs. 42, 43), form a distinct group based on pollen morphology. They are characterized by weakly defined apertures or apertural regions (sometimes absent in *Megistostigma*), a tectate-punctate exine with supratectal microverrucae, and an apertural sexine that is fragmented into small islands (Table 2). The primary differences among the genera are in the shape and size of the apertural sexine regions. *Pachystylidium* (Figs. 42, 43) has three circular, porelike apertures, whereas *Cnesmone* (Figs. 36, 39) typically has three elliptic colpuslike apertures. In *Megistostigma* (Fig. 40), the apertural condition varies from three (or four) colpuslike apertures to more randomly distributed apertural regions or sometimes inaperturate. *Megistostigma* is characterized by having an apertural condition that varies both between and within species (including within a single sample); *M. cordata* has pollen with either three colpuslike apertures as in *Cnesmone* or with randomly distributed irregular apertural regions, while *M. malaccense* is weakly and irregularly aperturate or inaperturate. Pollen evidence supports the hypothesis based on floral morphology that *Megistostigma* and *Cnesmone* are sister taxa. In fact, the two genera may not be as distinct as previously thought; the traditional distinctions of style morphology and presence of a staminate ap-

pendage appear to break down as more species are recognized and described. Pollen characters, as described above, cannot be used to separate the two genera. Since pollen of *Pachystylidium* is intermediate between pollen of *Cnesmone* and *Megistostigma* and pollen of several species of *Tragia* (*T. novae-hollandiae* and section *Leptobotrys*), pollen morphology does not strongly support either recognition of *Pachystylidium* as a distinct monotypic genus (following Pax & Hoffmann, 1919; Airy Shaw, 1969, 1975) or as a species of *Tragia* (following Webster, 1975). Pollen evidence does suggest a relationship with its geographical neighbors, *Megistostigma* and *Cnesmone*, despite a very different staminate flower morphology.

The Old World, predominantly African, taxa, *Tragia* sect. *Tagira* Muell. Arg. (Figs. 61 63), *Tragia* sect. *Lassia* (Figs. 59, 60), and *Tragiella* (Figs. 75-77) were found to share a similar pollen morphology (Table 2). Pollen is tricolpate with a reticulate tectum, a very uneven aperture margin, and scattered islands of sexine often present on the apertural membrane (apparently absent in *Tragiella*). Pollen evidence suggests that the three taxa are closely related and supports Webster's (1975) treatment of *Tragiella* as a synonym of *Tragia* (a new section within *Tragia* would be necessary to accommodate the species of *Tragiella*), rather than as a distinct genus (following Radcliffe-Smith, 1982, 1987). Section *Lassia* is morphologically very similar to *Tagira* and may not be distinct from that section; *Lassia* is distinguished by a single apomorphic androecial character. *Sphaerostylis* (not examined here) also has tricolpate pollen with a reticulate tectum similar to the above taxa according to observations by Punt (1962). This evidence is consistent with Croizat's (1941) hypothesis of a relationship with *Tragiella* (though differences in calyx and foliar morphology, as pointed out by Radcliffe-Smith (1987), would provide evidence against combining the two genera) rather than with *Megistostigma* (following Pax & Hoffmann, 1919).

Two African taxa of *Tragia* were found to have unique pollen types very different from the above African Tragiinae. *Tragia ivohibeensis* is an endemic Madagascan species for which Léandri (1971) created the monotypic subgenus *Mauroya*, apparently because he thought it intermediate between several genera including *Tragiella* and *Sphaerostylis*, and two sections of *Tragia*, *Agirta*, and *Ratiga*. Pollen morphology of *T. ivohibeensis* (Figs. 72 74), however, does not resemble either *Tragiella* or any species of *Tragia* examined. The apertures (usually three) are very poorly defined areas partially covered with fragments and strands of sexine (and usually not visible under LM). The tectum, both apertural and nonapertural, is reticulate but finer than in *Tragiella* and *Tragia* sect. *Tagira*. The species appears most similar in vegetative and floral morphology to the endemic Madagascan section *Agirta*, differing primarily in style morphology. Pollen of *Tragia* sect. *Agirta* needs to be examined to confirm this suggested relationship.

The second pollen type unique among African Tragiinae is found in the southern African taxon *Tragia* sect. *Ctenomeria* (Harv.) Benth. While resembling the majority of African Tragiinae in having pinnatifid pistillate sepals (a feature found only in the Old World), the section has a very distinct androecium of numerous stamens (30–50) with highly elongate anthers. Palynologically very distinct also, section *Ctenomeria* is characterized by weakly defined apertures (*tenuitates*), which may split in an irregular manner, and a reticulate tectum, which is often continuous but much thinner across the aperture (Figs. 51–54). This pollen type is unique in the tribe and cannot be easily related to other types, emphasizing the distinctness of section *Ctenomeria*. A somewhat similar pollen type is found in the isolated, monotypic South American genus *Dysopsis* (tribe Acalypheae) (Fernández-González et al., 1994); however, similarity with *Tragia* sect. *Ctenomeria* is most likely due to convergence.

Four distinct pollen types are found among neotropical species of *Tragia*. Section *Bia* is the only section of *Tragia* characterized by inaperturate pollen (Figs. 47–50). Pollen morphology together with inflorescence architecture and staminate flowers having disc segments and five to many stamens (5–20) emphasize the distinctness of section *Bia*, as was also pointed out by Punt (1962). A second pollen type is represented by *Tragia bailloniana* (Figs. 67–69) belonging to the monotypic section *Zuckertia* (Baill.) Muell. Arg. The tricolpate pollen of *T. bailloniana* is remarkably similar to pollen of *Plukenetia* (Figs. 14 24) and *Romanoa* (Figs. 25–27), differing from *Plukenetia* Type 2 pollen primarily in its more finely reticulate tectum and muri that are often scabrate but not crenate, and from *Romanoa* only in the larger size of the perforations. Baillon (1858) originally described the species as *Zuckertia cordata* and pointed to a similarity with *Romanoa*, while Miller & Webster (1967) suggested that the species was one of the most primitive in *Tragia*. Since presence of stinging hairs and a slender 3-branched style places *T. bailloniana* in *Tragia* and not in subtribe Pluke-

netiinae, pollen evidence supports the hypothesis that the species is one of the least derived members of *Tragia*. The section *Zuckertia* pollen type appears to represent the plesiomorphic condition in subtribe Tragiinae based on outgroup comparison with subtribe Plukenetiinae.

The majority of New World species of *Tragia* belong to section *Tragia*, which appears to be characterized by a single unique pollen type. Pollen of all species examined is tricolpate with an unusual, apparently intectate sexine consisting of baculate or clavate sculptural elements (Figs. 64–66). Pollen is similar to *Tragia* sect. *Tagira* in having apertures with very uneven margins and scattered islands of sexine on the apertural membrane, but differs in exine structure and broader colpi with usually fewer sexine islands. While described as operculae by Miller & Webster (1967) on the basis of LM observations, these apertural sexine islands are irregular in shape, size, and position, and therefore cannot be considered as operculae (according to Erdtman's (1952) definition of an operculum as a "thickening of measurable bulk and clearly defined of an aperture membrane (circular in pori, elongate in colpi . . .)"). Although only eight species of this large section were examined, LM observations by Punt (1962), Miller & Webster (1967), and R. Urtecho (pers. comm.) suggest that this pollen type is characteristic of section *Tragia* and represents the only occurrence of intectate pollen (sensu Walker & Doyle, 1975, i.e., excluding the semitectate condition considered by Punt, 1962, as intectate) in the tribe Plukenetieae.

Several sections included here in section *Tragia* are sometimes treated as distinct sections (Pax & Hoffmann, 1919, 1931). These include section *Ratiga* Muell. Arg. (which includes *Tragia chlorocaulon*, *T. mexicana*, and *T. tristis*), section *Leucandra* (*T. polyandra*, *T. ramosa*), and section *Leptorhachis* (Klotzsch) Muell. Arg. (resurrected by Múlgura de Romero & Gutiérrez de Sanguinetti (1989) for several South American species, including *T. polyandra*, but treated by Pax and Hoffmann under section *Leucandra*). Since these sections share the same pollen type as section *Tragia* (sensu Pax & Hoffmann; including *T. pacifica*, *T. peltata*, and *T. volubilis*), pollen morphology does not support their recognition as distinct sections.

The fourth pollen type among New World *Tragia* is found in *Tragia* sect. *Leptobotrys* (Figs. 55–58). Pollen has three poorly defined circular apertures with a very indistinct margin and covered with small, often conical or baculate islands of sexine. The distinct apertural condition, tectum morphology, and apertures densely covered with sexine islands support Miller & Webster's (1967) conclusions based on staminate flower morphology and LM observations of pollen that Mueller's section *Leptobotrys* is valid and should not be included in section *Tragia* (as done by Pax & Hoffmann, 1919).

Curiously, pollen of *Tragia* sect. *Leptobotrys* is most similar to pollen of *T. novae-hollandiae* (Figs. 70, 71), the only species of *Tragia* known from Australia (section undetermined; although Pax & Hoffmann (1919) included the species in section *Leucandra*, it is anomalous both in that section and section *Tragia*). The two taxa share a very similar aperture condition, tectum morphology, and obtuse-triangular shape (Table 2). Together they most closely resemble the southeast Asian genus, *Pachystylidium*, differing primarily in details of tectum morphology, both apertural and nonapertural. Airy Shaw (1969) pointed to a relationship between *T. novae-hollandiae* and *Pachystylidium* based on the shared state of subsessile anthers and suggested that the species is transitional between *Pachystylidium* and *Tragia*. In addition, *Tragia* sect. *Leptobotrys* and *Pachystylidium* share a stamen number of two, an unusual condition in the tribe. Whether similarity in pollen morphology between these three disjunct taxa is due to homology or convergence needs to be examined further.

APERTURE EVOLUTION IN TRIBE PLUKENETIEAE

Pollen synapomorphies defining the Plukenetieae are tricolpate aperture condition and uneven aperture margins. Tricolpate aperture condition is primitive in the tribe based on outgroup comparison with *Dalechampia* and the remainder of the subfamily Acalyphoideae. Throughout the Plukenetieae aperture margins are uneven and often appear fragmented, jagged, or frayed. The character state tree in Figure 78 illustrates one hypothesis of the evolution of aperture condition in the Plukenetieae, and will be discussed in greater detail below.

In subtribe Plukenetiinae aperture condition is uniformly tricolpate (Table 2, Fig. 78b). Variation in aperture morphology is primarily in colpus size and shape, presence of an elongate chamber within the exine next to the colpus, and presence of an apertural sexinous membrane.

In subtribe Tragiinae there has been an unusual radiation in aperture condition and morphology (Table 2). There is a distinct trend toward less well defined apertures and ultimately toward loss of apertures in several evolutionary lines. Aperture margins have become more irregular and less de-

fined, and fragments or distinct islands of sexine are often present on the apertural membrane.

The majority of species of *Tragia* are tricolpate; all of these species, with the exception of *T. bailloniana*, have scattered islands of sexine on the apertural membrane and very uneven margins (Fig. 78c). A single species of *Acidoton* (Type 1) also has pollen of this type.

Three different types of weakly defined apertures are found in the Tragiinae, each presumably originating independently from the tricolpate condition. One type consists of apertural areas densely covered with numerous small islands of sexine and with an exine equal in thickness or only slightly thinner than the nonapertural exine. These areas may be either elliptic (Fig. 78d; *Cnesmone*, Fig. 39, and *Megistostigma*), circular (Fig. 78g; *Pachystylidium*, Fig. 42, *Tragia* sect. *Leptobotrys*, Figs. 57, 58, and *T. novae-hollandiae*, Fig. 71), or irregular in shape (Fig. 78e; *Megistostigma*, Fig. 40). A second type of weakly defined aperture is represented by *Tragia* sect. *Ctenomeria* (Fig. 51), which has apertures covered with a continuous or sometimes fragmented, distinctly thinner exine, often visible as depressed areas (Fig. 78i). *Tragia* subg. *Mauroya* (Fig. 73) represents a third type characterized by very weakly defined apertures covered with strands of sexine continuous with and identical in sculpture to the nonapertural exine (Fig. 78j).

Inaperturate pollen appears to have evolved at least twice in subtribe Tragiinae. In the Old World, inaperturate pollen (Fig. 78f) evolved via weakly defined colpate (Fig. 78d) and irregularly aperturate grains (Fig. 78e) and is found only in *Megistostigma* (note that apertural condition is variable within the genus and within species, e.g., *M. malaccense* has both irregularly weakly aperturate and inaperturate grains, whereas *M. cordata* has both weakly tricolpate and irregularly aperturate grains). In the New World, inaperturate pollen (Fig. 78h) originated one or more times most probably from tricolpate pollen having scattered sexine islands on the apertural membrane (Fig. 78c) and is found in three taxa, *Platygyna* (Fig. 44), *Acidoton* Type 2 (Figs. 34, 35), and *Tragia* sect. *Bia* (Figs. 47, 49). An alternative hypothesis would be origin directly from tricolpate grains lacking apertural sexine islands (Fig. 78b). *Acidoton* Type 2 (and possibly *Platygyna*) pollen most likely originated from *Acidoton* Type 1, i.e., pollen having narrow colpi with numerous sexine islands, whereas there is no strong evidence either way for the origin of inaperturate pollen in *Tragia* sect. *Bia*.

Conclusions

The use of SEM in the present study of pollen morphology of the Plukenetieae has provided a much greater number of systematically useful characters than was possible with LM alone. In particular, details of tectum morphology were much more highly resolved and enabled detection of unusual apertural conditions and morphology. Several taxa, not considered to represent distinct pollen types in Punt's (1962) study based on LM alone, were distinct when viewed under SEM. These include *Tragia capensis* grouped by Punt with the *Plukenetia volubilis* subtype, *Tragiella* and *Tragia* sect. *Tagira* grouped with the *Plukenetia verrucosa* subtype, and *Acidoton* included in the *Cnesmosa* type with *Cnesmone* and *Megistostigma*.

The tricolporate, coarsely reticulate pollen of *Dalechampia* supports the hypothesis of *Dalechampia* as the sister taxon of the Plukenetieae (as circumscribed here), rather than being derived from within the tribe. Webster's (1994) treatment of the genus as a subtribe within the Plukenetieae is consistent with either hypothesis.

Pollen evidence is consistent with Webster's (1975) division of tribe Plukenetieae into two subtribes, Plukenetiinae and Tragiinae, but does not support Pax & Hoffmann's (1919) division into four informal groups. Of these groups only Astrocciformes (comprising *Astrococcus* and *Haematostemon*) is monophyletic, Tragiiformes (*Tragia*) is paraphyletic, while Plukenetiiformes (most Plukenetiinae plus *Acidoton* and *Platygyna*) and Sphaerostyliformes (all other Tragiinae) appear to be polyphyletic.

Pollen morphology supports a subdivision of subtribe Plukenetiinae into an arborescent group (*Angostyles*, *Astrococcus*, and *Haematostemon*) and a lianous group (*Plukenetia* and *Romanoa*). Also supported is the recent synonymy of *Vigia* and *Eleutherostigma* under *Plukenetia* (Gillespie, 1993), and the relationship of *Astrococcus* and *Haematostemon* as sister taxa.

Subtribe Tragiinae exhibits an exceptionally diverse pollen morphology, with much of the variation present in the large genus *Tragia*. Pollen morphology, for the most part, supports the sectional classification of *Tragia*. The two largest sections, neotropical *Tragia* and paleotropical *Tagira*, have tricolpate pollen with scattered sexine islands on the apertural membrane, but are easily distinguished based on exine morphology. Of the remaining taxa, sections *Bia*, *Ctenomeria*, *Leptobotrys*, and *Zuckertia*, and subgenus *Mauroya* are

each characterized by a unique pollen type, providing evidence that they are indeed distinct natural groups. Pollen evidence does not support *Lassia* as a section distinct from *Tagira*, but does support the inclusion of sections *Leucandra*, *Leptorhachis*, and *Ratiga* within section *Tragia*. The hypothesis of section *Zuckertia* as a plesiomorphic member of *Tragia* is supported.

The remaining genera in subtribe Tragiinae, for the most part, are characterized by unique pollen types distinct from *Tragia*. The southeast Asian taxa, *Megistostigma* and *Cnesmone*, form a distinct group based on pollen morphology that is most similar to pollen of *Pachystylidium*. Pollen evidence is consistent with the status of *Platygyna* as a genus distinct from *Tragia*. *Acidoton* includes two different pollen types, inaperturate and tricolpate; the close similarity of inaperturate Type 2 pollen to pollen of *Platygyna* suggests that *Acidoton* may not be monophyletic. *Tragiella* has pollen very similar to *Tragia* sect. *Tagira*, and would perhaps be best considered a section of *Tragia* related to section *Tagira*.

Pollen and floral morphological evidence indicate that a major reorganization of generic delimitations may be necessary in the Tragiinae to better reflect phylogenetic relationships. *Tragia* appears to be a highly paraphyletic genus as presently circumscribed. Most of the remaining Tragiinae genera appear to be derived with respect to *Tragia* and defined on the basis of unusual and presumably apomorphic style and androecium characters (and also by apomorphic pollen characters). Pollen evidence frequently suggests a close relationship among geographical neighbors, a relationship that is not reflected in the current classification. To ensure a phylogenetic classification, it may be necessary to subdivide *Tragia* and recognize certain sections, such as *Bia* and *Ctenomeria*, as distinct genera (as they have been treated in the past, e.g., Baillon, 1858), since these sections are as distinct as most Tragiinae genera. An alternative but more cumbersome approach would be to combine most Tragiinae genera into *Tragia* with a complex system of subgenera and sections to indicate relationships. The level at which taxa such as *Tragiella*, *Pachystylidium*, and *Platygyna* are recognized will depend on which approach is followed.

The present study should not be regarded as exhaustive; some taxa need to be more thoroughly surveyed, particularly the two largest sections of *Tragia*, *Tagira* and *Tragia* (to verify that only a single pollen type is found in each), while several Madagascan taxa still need to be examined. The hypotheses of phylogenetic relationships suggested in this paper need to be further tested by means of cladistic studies using floral, vegetative, and pollen characters. Taxa sharing a similar pollen morphology, but not previously thought to be closely related, need to be more thoroughly examined to determine if these similarities are homologous or the result of convergence. A more complete understanding of the phylogeny of subtribe Tragiinae is recommended prior to making specific changes in the generic and sectional classification.

Literature Cited

Airy Shaw, H. K. 1968. Notes on Malesian and other Asiatic Euphorbiaceae. XCII. Note on the affinity of *Ramelia* Baill. Kew Bull. 21: 401–403.

———. 1969. Notes on Malesian and other Asiatic Euphorbiaceae. CXII. Notes on the subtribe Plukenetiinae Pax. Kew Bull. 23: 114–121.

———. 1974. Notes on Malesian and other Asiatic Euphorbiaceae. CXII. New or noteworthy species of *Bocquillonia* Baill., with a revised key to the genus. Kew Bull. 29: 315–322.

———. 1975. The Euphorbiaceae of Borneo. Kew Bull. Add. Ser. IV.

Armbruster, W. S. 1994. Early evolution of *Dalechampia* (Euphorbiaceae): Insights from phylogeny, biogeography, and comparative ecology. Ann. Missouri Bot. Gard. 81: 302–316.

Baillon, H. E. 1858. Etude générale du groupe des Euphorbiacées. Victor Masson, Paris.

Bentham, G. 1880. Euphorbiaceae. *In:* G. Bentham & J. D. Hooker (editors), Genera Plantarum ad Exemplaria Imprimis in Herbariis Kewensibus Servata Definita 3: 239–340. Lovell Reeve, London.

Borhidi, A., J. Acuna & G. Muniz. 1973. New plants in Cuba III. Acta Bot. Acad. Sci. Hung. 19: 37–45.

Croizat, L. 1941. The tribe Plukenetiinae of the Euphorbiaceae in eastern tropical Asia. J. Arnold Arbor. 22: 417–431.

Erdtman, G. 1952. Pollen Morphology and Plant Taxonomy. Angiosperms. Almqvist & Wiksell, Stockholm.

———. 1966. Pollen Morphology and Plant Taxonomy. Angiosperms (corrected reprint of the 1952 edition with a new addendum). Haffner, New York.

Fernandez-Gonzalez, D., M. Suarez-Cervera & A. Le Thomas. 1994. Ultrastructure du pollen de *Dysopsis* Baill.: Relations phylogénetiques au sein des Acalypheae (Euphorbiaceae). Acta Botanica Gallica 141 (in press).

Gillespie, L. J. 1988. A revision and phylogenetic analysis of *Omphalea* (Euphorbiaceae). Unpublished Ph.D. Dissertation. University of California, Davis.

———. 1993. A synopsis of neotropical *Plukenetia* (Euphorbiaceae) including two new species. Syst. Bot. 18: 575–592.

Greuter, W. et al. (editors). 1988. International Code of Botanical Nomenclature. Regnum Veg. 118.

Köhler, E. 1965. Die Pollenmorphologie der biovulaten Euphorbiaceae und ihre Bedeutung für die Taxonomie. Grana Palynol. 6: 26–120.

LÉANDRI, J. 1971. Un sous-genre malgache nouveau de *Tragia* (Euphorbiacées). Adansonia, sér. 2. 13: 437–439.

LEVIN, G. A. & M. G. SIMPSON. 1994. Phylogenetic implications of pollen ultrastructure in the Oldfieldioideae (Euphorbiaceae). Ann. Missouri Bot. Gard. 81: 203–238.

LIOGIER, A. H. 1971. Novitates Antillanae IV. Euphorbiaceae. Mem. New York Bot. Gard. 21: 123–133.

LYNCH, S. P. & G. L. WEBSTER. 1975. A new technique of preparing pollen for scanning electron microscopy. Grana 15: 127–136.

MILLER, K. I. & G. L. WEBSTER. 1967. A preliminary revision of *Tragia* (Euphorbiaceae) in the United States. Rhodora 69: 241–305.

MULGURA DE ROMERO, M. E. & M. M. GUTIERREZ DE SANGUINETTI. 1989. Actualización taxonómica de *Tragia* (Euphorbiaceae) para Argentina y regiones limítrofes. Darwiniana 29: 77–138.

NOWICKE, J. 1994. A palynological study of Crotonoideae (Euphorbiaceae). Ann. Missouri Bot. Gard. 81: 245–269.

PAX, F. A. & K. HOFFMANN. 1919. Euphorbiaceae–Plukenetiinae. *In:* A. Engler (editor), Das Pflanzenreich IV.147.XI. (Heft 68): 1–108. W. Engelmann, Leipzig.

——— & ———. 1924. Euphorbiaceae—Additamentum IV. *In:* A. Engler (editor), Das Pflanzenreich IV.147.XV11. (Heft 85): 179–204. W. Engelmann, Leipzig.

——— & ———. 1931. Euphorbiaceae. *In:* A. Engler & K. Prantl (editors), Die Natürlichen Pflanzenfamilien, ed. 2, 19c: 11–233. W. Engelmann, Leipzig.

PUNT, W. 1962. Pollen morphology of the Euphorbiaceae with special reference to taxonomy. Wentia 7: 1–116.

RADCLIFFE-SMITH, A. 1980. A note on *Romanoa* (Euphorbiaceae). Kew Bull. 34: 591–592.

———. 1982. Notes on African Euphorbiaceae: XIII. Kew Bull. 37: 683–691.

———. 1987. Euphorbiaceae (Part 1). *In:* R. M. Polhill (editor), Flora of Tropical East Africa. A. A. Balkema, Rotterdam.

RADFORD, A. E., W. C. DICKISON, J. R. MASSEY & C. R. BELL. 1974. Vascular Plant Systematics. Harper & Row, New York.

TREVISAN, V. B. A. 1848. Saggio di una monografia delle alghe Coccotalle. Padova.

WALKER, J. W. & J. A. DOYLE. 1975. The bases of angiosperm phylogeny: Palynology. Ann. Missouri Bot. Gard. 62: 664–723.

WEBSTER, G. L. 1967. *Acidoton* (Euphorbiaceae) in Central America. Ann. Missouri Bot. Gard. 54: 191.

———. 1975. Conspectus of a new classification of the Euphorbiaceae. Taxon 24: 593–601.

———. 1994. Synopsis of the genera and suprageneric taxa of Euphorbiaceae. Ann. Missouri Bot. Gard. 81: 33–144.

——— & W. S. ARMBRUSTER. 1991. A synopsis of the neotropical species of *Dalechampia* (Euphorbiaceae). J. Linn. Soc. Bot. 105: 137–177.

——— & B. D. WEBSTER. 1972. The morphology and relationships of *Dalechampia scandens* (Euphorbiaceae). Amer. J. Bot. 59: 573–586.

CONTRIBUTIONS TOWARD A MONOGRAPH OF NEOTROPICAL *JATROPHA*: PHENETIC AND PHYLOGENETIC ANALYSES[1]

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Abstract

Phenetic analysis of the New World *Jatropha* L. species generally supports the 1979 classification of the genus by Dehgan and Webster. The distinctness of subgenera *Curcas* (Adans.) Pax and *Jatropha*, the intermediate position of section *Polymorphae* Pax between sections of both subgenera, and the close relationship of sections *Mozinna* (Ortega) Pax and *Loureira* (Cav.) Muell. ex Pax are indicated. Phylogenetic analysis provided evidence of monophyly for subgenus *Jatropha*, sections *Jatropha* and *Mozinna*, and probable paraphyly in subgenus *Curcas* and several sections and subsections. The cladistic analyses described herein produced multiple parsimonious topologies. The circumscriptions of the subgenera and some sections and subsections are significantly clarified. The status of heretofore dubiously placed or recently described species is also elucidated. Although geographical data were not included in the phylogenetic analyses, a distinct correlation between evolutionary trends in morphological features, postulated infrageneric delimitations, and geography of the genus became evident. Evidence is presented to support the antiquity of the genus and its present distribution, which resulted from a Gondwanaland breakup and subsequent overland dispersal across the African and American continents. Adaptive gradual mosaic evolution as a series of successive speciational steps, primarily involving morphological features, in concert with migration to areas of increasing aridity and cold appears to be the norm for the genus.

Adanson (1763) was the first to note that *Jatropha* has proceeded along two evolutionary lines when he recognized the two genera *Jatropha* and *Curcas*, based on Linnaeus's *Species Plantarum* (1763). Although Adanson's generic delimitation proved incompatible with that of later taxonomists (Pohl, 1827; Baillon, 1858; Mueller Argoviensis 1874; Pax, 1910), its basic premise was retained through consolidation and reduction of the two genera to subgenera and/or sections. The gamopetalous nature of the corolla in *Curcas* and its distinctness in *Jatropha* had generally been used as justification for recognition of these groups. McVaugh (1945) was the first to discard the two groups and pointed out the danger of constructing a classification based on a single corolla character. He proposed four "homogeneous" sections for the American species. Dehgan & Webster (1979) accepted and incorporated, with minor modifications, three of McVaugh's four sections into their revised system and recognized them as distinct sections of the subgenus *Jatropha*. Section *Mozinna* (Ortega) Pax was regarded as more or less equivalent to the subgenus *Curcas* (Adans.) Pax of Dehgan & Webster (1979), which itself now includes four sections. This classification was supported primaily by gross morphology of reproductive structures. A brief review of Dehgan and Webster's classification seems appropriate for better understanding of the results of this study and is presented below.

Two subgenera (*Curcas* and *Jatropha*), ten sections, and ten subsections were recognized to accommodate the Old and New World species. The subgenera were distinguished by growth habit, calyx aestivation, corolla coherence or connation, plant sexuality (monoecious or dioecious), stamen number and arrangement, seed shape, and presence or absence of a caruncle. It was postulated that *J. curcas* L. [sect. *Curcas* (Adans.) Griseb., subg. *Curcas* (Adans.) Pax], retains the most plesiomorphic, or "primitive," features of any species in the genus, notably its palmately lobed leaves,

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arborescent growth habit, possession of a discrete coflorescence (a distinct basal-lateral branch of the main-florescence), and occasional hermaphroditic flowers, among other characteristics, including several anatomical features that it shares with members of both subgenera. Evolution from it or a similar ancestral taxon involved changes in growth habit, including loss of arborescence coupled with the acquisition of either a facultative annual growth habit, exemplified by *J. gossypiifolia* L. (sect. *Jatropha*, subg. *Jatropha*), or a rhizomatous subshrub habit, shown by some species of section *Mozinna* (Ortega) Pax, (subg. *Curcas*). These changes were accompanied by a series of reductions in reproductive structures of both subgenera. The evolutionary trends of the inflorescence apparently followed two distinct pathways. On the one hand, modification and ramifications of coflorescences and paracladia (inflorescence branches) resulted in the formation of a highly symmetrical compound dichasium, via section *Polymorphae* Pax, in section *Peltatae* (Pax) Dehgan & Webster (both strictly American) or the coflorescence was reduced to a single pistillate flower in the African section *Collenucia* (Chiov.) Chiov. On the other hand, inflorescences became markedly reduced to a few or solitary flowers in section *Mozinna*, subgenus *Curcas*, in concert with a gradual shift from monoecy to gynodioecy and dioecy. These modifications were often accompanied by changes in chromosome numbers, from diploidy to tetraploidy, nearly always accompanied by acquisition of rhizomatous growth habit. Evolution of the flowers also proceeded in two very different directions. In subgenus *Jatropha*, reduction and rearrangement of stamens has occurred, from ten to eight and from uniseriate to biseriate, connate to free, with no concomitant change in the number of styles and locules of the ovary, all with three bifurcate styles and 3-locular ovary (with the notable exception of two bifurcate styles of *J. martiusii* (Pohl) Baillon). In contrast, the number and arrangement of stamens in the American taxa of subgenus *Curcas* has remained consistently ten, but the number of locules, seeds, and style branches have been gradually reduced from three (in sects. *Curcas* and *Platyphyllae* Dehgan & Webster), to two (in most members of sect. *Loureira* (Cav.) Mull. Arg. ex Pax), and one (in several species of sect. *Mozinna* (Ortega) Pax). In general, these changes exhibit a morphological continuum from south to north, with the southern taxa possessing the more primitive and the northern species the more advanced features.

Several anatomical and micromorphological features support this classification. Both articulated and nonarticulated laticifers are present in members of the subgenus *Jatropha*, but nonarticulated laticifers are lacking from all taxa in sections *Curcas* and *Platyphyllae*. Idioblastic laticifers and chambered crystalliferous parenchyma are characteristic of taxa in subgenus *Curcas* but completely absent from members of the subgenus *Jatropha* (Dehgan & Craig, 1978). Leaf surface morphology indicates the presence of brachyparacytic stomata in subgenus *Jatropha* and the true paracytic type in subgenus *Curcas*. Epidermal hairs of most taxa in subgenus *Jatropha* are uniseriate-multicellular and smooth, while those of subgenus *Curcas* are unicellular and verrucate (Dehgan, 1980; Olowokudejo, 1993). The number and arrangement of petiolar vascular bundles vary from (11–)9, 7, 5, and 3 in a ring, as free traces, medullated cylinder, or U-shaped free or medullated free traces (Dehgan, 1982).

In hybridization studies, Dehgan (1984) presented evidence that taxa further apart in the revised evolutionary classification were progressively less capable of interbreeding than more closely positioned taxa. Related species were shown to have a high degree of unilateral compatibility but to be separated by preferential fertilization, whereas the more phylogenetically distant taxa were incompatible. *Jatropha curcas* L., which, in agreement with McVaugh (1945) and Wilbur (1954), was considered the most primitive species on morphological and anatomical grounds, proved most compatible with species of sections with presumably closest affinity (e.g., *J. integerrima* Jacq. of sect. *Polymorphae*), and least compatible with taxa of the more advanced sections (e.g., *J. gossypiifolia* of sect. *Jatropha* and *J. dioica* Sessé, of sect. *Mozinna*). It was concluded that in *Jatropha* phylogenetic distance may be reflected by ability of the species to interbreed.

Despite these convincing lines of evidence supporting alignment of the taxa, placement of some species remained somewhat dubious. Scarcity of living plants, incomplete herbarium specimens, and insufficient knowledge of the South American taxa (sects. *Jatropha* and *Peltatae*) were among the reasons for doubtful placement of several species. With the senior author's recent extensive field collections in Brazil and Mexico, reappraisal and or confirmation of Dehgan & Webster's (1979) revision, using all available information for the neotropical taxa, seemed appropriate. The authors were also interested in examining the present taxonomic delimitation and assessment of relationships through

interpretation of the results of phenetic and cladistic analyses. The intent of this paper is not to present a cladistic classification of the New World taxa; we know that New World jatrophas do not constitute a strictly monophyletic group, and that Old World taxa must be included to create a new cladistic classification. Thus, we have used both cladistic and phenetic techniques to examine the current traditional morphology-based classification for corroborative purposes only. With a brief discussion of geography and evolution added, this report is intended as a contribution toward a monographic treatment of the neotropical species in the near future.

A. Ordination and Hierarchical Cluster Analysis

Materials and Methods

Principal component ordination and hierarchical cluster analysis of living and herbarium specimens of 93 taxa (subsequently reduced to 77 based on later assessments of synonymy) representing all New World species, and 32 characters (see Appendix for vouchers, Table 1 for characters) were performed using F. J. Rohlf's NTSYS-pc multivariate statistical program package (version 1.4). The data matrix of 77 taxa by 32 characters is shown in Table 2. Although this program provides three-dimensional scattergrams, two- and three-dimensional scattergrams were constructed from PCA factor scores using a computer program written by the second author. Among other features, this program has the distinct advantage of enabling the user to identify individual taxa by their identification number in the data matrix. It also has the ability to "zoom in" on and enlarge selected areas of the PCA scattergram so that the identity of closely spaced taxa in the diagram may be more easily resolved. Data matrices are input to the NTSYS-pc program, which standardizes the raw data ("z-score" method of Sneath & Sokal, 1973), calculates eigenvectors, and projects them onto axes for display. Schutzman's program can read and display the projection output files from NTSYS-pc with only minor modifications.

Results and Discussion

The results of PCA and hierarchical cluster analyses (Figs. 1–4) for the most part confirmed the earlier infrageneric classification of Dehgan & Webster (1979). Factor loadings, signifying the most meaningful characteristics for each principal component in each of the three PCAs, were calculated and are listed in Table 3A–C. Two discrete groups of OTUs corresponding to subgenera *Jatropha* and *Curcas* were apparent at the outset (Figs. 1 and 4). The centralized, unifying position of section *Polymorphae* had already been predicted and illustrated by Dehgan (1984). The affinity of this section with both subgenera became more apparent when species of *Polymorphae* were included in both data sets and analyzed independently (Figs. 2 and 3). In addition to their past (see the discussion below) and present geographical affiliation (Mesoamerica and West Indies), it was shown earlier (Dehgan, 1984) that *J. integerrima* and *J. curcas* are highly compatible and produce fertile progeny when artificially crossed. In fact, there is considerable phenetic similarity between sections *Curcas* and *Polymorphae*. The presence of 10 connate biseriate stamens, connation and/or imbrications of the petals, and similarity of leaf morphology are but a few of the reasons for such relationship. The affinity of *J. hernandiifolia* Vent., *J. divaricata* Sw. (both West Indian), and *J. gaumeri* Greenm. (endemic to the Yucatan Peninsula), species placed by Dehgan & Webster (1979) in subsection *Hernandiifoliae* Dehgan & Webster of section *Polymorphae*, has also been confirmed by the results of the phenetic analyses presented here. Recognition of a distinct subsection was based on the seven petiolar traces with secondary growth, corymbose inflorescence without a coflorescence, and campanulate pistillate flowers with imbricate petals. However, their placement with species previously grouped under section *Platyphyllae* in the PCA and cluster analyses (Figs. 1–4) was suspected on morphological and geographical grounds and appears quite reasonable. Except for the unique inflorescences of *J. hernandiifolia* and *J. divaricata*, nearly all other features, including white flowers, number and arrangement of stamens, features of the perianth, and entire nonglandular leaves, are very similar among the taxa in this section.

Reasons for probable derivation of species in section *Mozinna* from those of section *Loureira* based on morphological-anatomical features were discussed by Dehgan & Webster (1979) and by Dehgan & Craig (1978) and Dehgan (1980, 1982, 1984). The plausibility of such relationship is further strengthened by the results of both phenetic and cladistic analyses and is examined further below. Affinities of a few other species, such as *J. moranii* Dehgan & Webster (endemic to a small area in Baja California), *J. bullockii* Lott (with 8 biseriate stamens, endemic to higher elevations of

TABLE 1. Characters and character states for ordination and hierarchical cluster analysis.

1. Growth form:	Trees (0), shrubs (1), subshrubs (2). Based on strict botanical definition a tree is assumed to be in excess of 5 meters, a shrub 1–5 meters, and a subshrub less than 1 meter.
2. Caudiciform habit:	Plants geophytes (1), plants typical (0). Plants with thickened subterranean stems (a subterranean caudex).
3. Rhizomatous habit:	Plants rhizomatous (1), plants typical (0), Plants with spreading rhizomes.
4. Plant sex:	Dioecious (1), monoecious (0).
5. Laticifers:	Articulated and/or nonarticulated (1), idioblastic (0). Some species possess both articulated and nonarticulated laticifers but only some have idioblastic type.
6. Laticifers:	Nonarticulated (1), articulated (0). Plants may have both articulated and non-articulated laticifers but nonarticulated absent from some.
7. Leaf outline:	Lanceolate (0), ovate-lanceolate (1), ovate-elliptic (2), cordate-reniform (3), ob-ovate (4). A general outline of whole leaves regardless of lobing.
8. Leaf base:	Peltate (1), not peltate (0).
9. Leaf basal glands:	Present (1), absent (0). Basal glands are considered present even if the entire leaf margin is beset with stipitate glands.
10. Leaf margins:	Toothed (1), entire (0).
11. Leaf marginal glands:	Ciliate-glandular (1), eglandular (0). Margins may be toothed or entire and may or may not have glands.
12. Leaf sinus depth:	Parted (1), not parted (0). Leaves may be shallowly lobed but not necessarily parted.
13. Leaf lobe numbers:	Unlobed (0), 3- (3); 5- (5); 7- (7); 9-lobed (9). Infrequent occurrences of lobed leaves in plants with typically unlobed leaves have been ignored.
14. Leaf veins:	Palmate (1), pinnate (0).
15. Petioles:	Long (1), subsessile (0).
16. Petiolar traces:	3 (3), 5 (5), 7 (7), 9 (9), 11 (11).
17. Stipules:	Absent or fugacious (0), foliar (1), glandular-ciliate (2), filiform (3).
18. Hairs:	Absent (0), unicellular (1), uniseriate-multicellular (2).
19. Coflorescences:	Present (1), absent (0).
20. Flower shape:	Campanulate (0), rotate (1), tubular or urceolate (2).
21. Flower color:	White (1), other (0). This refers to absolute white flowers as opposed to yellow-ish or greenish white, and other colors.
22. Petals of ♀ flowers:	Distinct (0), imbricate (1), connate (2).
23. Petals of ♂ flowers:	Distinct (0), imbricate (1), connate (2). Frequently there is no correspondence between condition of the petals in the male and female flowers. The corolla may be distinct in the female but connate in the male.
24. Stamen arrangement:	Monadelphous (1), diadelphous (0).
25. Stamen number:	8 (1), 10 (0). Occasional odd stamen numbers have been ignored.
26. Stamen fusion:	Free (1), connate (0). Stamens have been considered connate even if only the central group is connate but the outer is free.
27. Style fusion:	Free (1), connate (0).
28. Calyx of ♀ flowers:	Foliaceous (1), not foliaceous (0). This refers only to the unusually large, leaf-like sepals.
29. Calyx lobe margins:	Glandular (1), entire (0).
30. Fruit dehiscence:	Violently dehiscent (1), tardily dehiscent (0). Fruit may explode upon maturity or remain intact for a considerable length of time.
31. Fruit locule number:	1 (1), 2 (2), 3 (3).
32. Seed:	Carunculate (1), ecarunculate (0).

a small area in Jalisco, Mexico), and *J. purpurea* Rose (narrow endemic in western Mexico), are also discussed below. Other than these few changes the basic delineation of Dehgan & Webster's (1979) infrageneric classification remains intact, but the necessity to create new monotypic sections for such species as *J. martiusii* will also be further elucidated.

B. CLADISTIC ANALYSIS

MATERIALS AND METHODS

Cladistic analyses were performed on the data set of 77 evolutionary units (EUs) and 31 characters using Hennig86 (James Farris, Department of Ecology and Evolution, State University of New York, Stony Brook, 1988) version 1.5. The char-

TABLE 2. Matrix of character states for 77 *Jatropha* species used in the phenetic analysis.

Taxon	Characters																														
	0 1	0 2	0 3	0 4	0 5	0 6	0 7	0 8	0 9	1 0	1 1	1 2	1 3	1 4	1 5	1 6	1 7	1 8	1 9	2 0	2 1	2 2	2 3	2 4	2 5	2 6	2 7	2 8	2 9	3 0	3 1	3 2
alamanii	0	0	0	1	1	1	3	0	0	0	0	0	5	0	1	07	0	0	0	2	1	2	0	0	0	0	0	1	0	0	3	0
andrieuxii	1	0	0	1	0	0	3	0	0	1	0	0	7	0	1	09	3	1	1	0	1	2	0	0	0	0	0	0	0	0	3	0
angustifolia	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	07	0	0	0	1	0	1	1	0	0	0	0	0	0	1	3	1
augustii	1	0	0	0	1	1	3	1	1	0	1	0	5	0	1	07	3	0	0	1	0	0	0	1	1	0	0	0	0	1	3	1
bartlettii	0	0	0	1	0	0	3	0	0	1	0	0	5	0	1	09	3	1	1	0	1	0	1	0	0	0	0	1	1	0	3	0
bullockii	1	0	0	0	0	0	3	0	0	0	0	0	3	0	1	05	0	0	0	2	1	2	0	0	1	0	0	0	0	1	3	1
canescens	1	0	0	1	1	1	2	0	0	0	0	0	0	0	1	05	0	1	0	2	0	2	2	0	0	0	0	1	0	0	2	0
cardiophylla	2	0	1	1	1	1	3	0	0	0	0	0	0	0	1	05	0	0	0	2	0	2	2	0	0	0	0	0	0	0	1	0
cathartica	2	1	0	0	0	0	3	0	0	0	0	1	7	0	1	09	3	0	0	1	0	0	0	1	1	1	1	0	0	1	3	0
chamelensis	0	0	0	1	1	1	2	0	1	0	0	0	0	0	1	09	0	0	0	2	1	0	2	0	0	0	0	1	0	1	3	0
ciliata	1	0	0	1	1	1	3	0	1	1	1	0	5	0	1	07	0	0	0	2	1	2	2	0	0	0	0	0	0	1	3	0
cinerea	1	0	0	1	1	1	3	0	0	0	0	0	3	0	1	05	0	1	0	2	0	2	2	0	0	0	0	1	0	0	2	0
clavuligera	1	0	0	0	0	1	2	0	1	0	1	1	7	0	1	07	2	2	1	0	0	0	0	0	0	0	0	1	0	1	1	3	1
cordata	0	0	0	1	1	1	3	0	1	0	1	0	0	1	1	07	2	0	0	2	0	2	2	0	0	0	0	1	1	0	2	0
costaricensis	0	0	0	1	0	0	2	0	0	0	0	0	5	0	1	07	0	1	1	2	1	2	2	1	0	0	0	1	0	0	3	0
cuneata	1	0	0	1	1	1	2	0	0	0	0	0	3	2	0	03	0	0	0	2	1	2	2	0	0	0	0	0	0	0	1	0
curcas	0	0	0	0	0	0	3	0	0	0	0	0	5	0	1	09	0	0	1	0	1	0	2	0	0	0	0	0	0	0	3	0
dioica	2	0	1	1	1	1	2	0	0	0	0	0	3	2	0	03	0	0	0	2	0	2	2	0	0	0	0	0	0	0	1	0
dissecta	2	1	0	0	0	1	3	0	1	0	1	1	5	0	1	07	2	2	1	1	0	0	0	1	1	0	1	0	1	1	3	1
divaricata	0	0	0	0	0	1	2	0	0	0	0	0	0	1	1	07	0	0	0	2	1	0	0	0	0	0	0	0	0	1	3	1
eglandulosa	2	0	0	0	0	1	2	0	0	0	0	0	0	1	0	07	3	2	1	0	0	0	0	1	1	1	0	0	0	1	3	1
elbae	1	0	0	1	1	1	2	0	0	0	0	0	0	2	0	03	0	0	0	2	1	2	2	0	0	0	0	0	0	0	1	0
elliptica	2	1	0	0	0	1	2	0	1	0	1	0	0	1	0	07	2	2	1	0	0	2	0	1	1	0	0	0	1	1	3	1
excisa	1	0	0	0	0	1	2	0	1	0	1	0	5	0	1	07	2	1	1	0	0	0	0	0	0	0	1	0	1	1	3	1
flavovirens	1	0	0	0	0	1	2	0	1	0	1	1	3	0	1	07	2	2	1	0	0	0	0	0	1	0	1	0	1	1	3	1
fremontioides	2	0	0	0	1	1	2	0	0	0	0	0	3	0	0	05	0	1	0	2	0	2	0	0	0	0	0	0	0	1	3	1
galvanii	0	0	0	1	1	1	3	0	0	0	0	0	0	0	1	07	0	0	0	0	0	0	0	0	0	0	0	1	1	0	2	0
gaumeri	0	0	0	0	0	0	2	0	0	0	0	0	0	0	1	07	0	0	0	2	1	2	2	1	1	0	1	0	0	1	3	1
giffordiana	1	0	0	1	1	1	3	0	0	0	0	0	0	0	1	05	0	1	0	2	0	2	2	0	0	0	0	1	0	0	3	0
gossypiifolia	1	0	0	0	0	1	3	0	1	0	1	0	5	0	1	07	2	2	1	0	0	0	0	0	1	0	0	0	1	1	3	1
grossidentata	1	0	0	0	0	1	2	0	0	1	0	0	5	0	1	07	0	0	0	1	0	0	0	1	1	1	1	0	0	1	3	1
guaranitica	2	1	0	0	0	1	3	0	1	0	1	0	3	0	1	07	2	2	1	0	0	0	0	0	1	0	1	0	1	1	3	1
hernandiifolia	0	0	0	0	0	0	2	1	0	0	0	0	3	0	1	07	0	0	0	2	1	1	2	0	0	0	0	0	0	1	3	1
hieronymii	0	0	0	0	0	1	3	0	0	1	0	0	5	0	1	07	2	0	0	1	0	0	0	1	1	1	1	0	0	1	3	1
hintonii	0	0	0	0	0	0	3	0	0	0	0	0	3	0	1	09	0	1	1	0	1	0	1	0	0	0	0	0	0	0	3	1
humboldtiana	1	0	0	0	0	1	3	1	1	0	1	0	0	0	1	07	2	0	0	1	0	0	0	1	1	1	0	0	0	1	3	1
integerrima	1	0	0	0	0	0	2	0	0	0	0	0	3	0	1	07	3	0	0	1	0	1	1	0	0	0	0	0	0	1	3	1
intercedens	1	0	0	0	0	1	2	0	1	0	1	0	3	0	1	07	2	2	1	0	0	0	0	0	1	0	0	0	1	1	3	1
intermedia	2	1	0	0	0	1	2	0	1	0	1	0	0	1	0	07	2	2	1	0	0	0	0	0	1	0	1	0	1	1	3	1
isabellii	2	1	0	0	0	1	2	0	1	0	1	0	0	1	0	07	2	2	1	0	0	0	0	0	0	0	1	0	1	1	3	1
katharinae	1	0	0	0	0	1	3	0	1	0	1	0	3	0	1	07	2	2	1	0	0	0	0	0	1	0	1	0	1	1	3	1
macrantha	2	0	0	0	0	1	3	0	0	0	0	0	3	0	1	07	1	0	0	1	0	0	0	1	0	0	0	0	0	1	3	1
macrocarpa	0	0	0	0	0	1	2	0	0	0	0	1	5	0	1	07	0	0	0	1	0	0	0	0	1	0	1	0	0	1	3	1
macrorhiza	2	1	0	0	0	1	3	0	0	1	0	1	7	0	1	07	3	0	0	1	0	0	0	0	1	0	1	0	0	1	3	1
malacophylla	0	0	0	1	0	0	3	0	0	1	0	0	5	0	1	09	0	1	0	0	1	2	2	1	0	0	0	1	0	0	3	0
martiusii	1	0	0	0	0	1	2	0	0	0	0	1	5	0	1	07	2	0	0	2	0	2	2	0	1	0	1	0	1	1	3	1
mcvaughii	0	0	0	1	0	0	3	0	0	0	0	0	7	0	1	09	0	1	1	0	1	2	2	1	0	0	0	0	0	0	3	0
mollissima	0	0	0	0	0	1	3	0	0	0	0	0	5	0	1	07	2	1	0	1	0	0	0	1	1	1	1	0	1	1	3	1
moranii	1	0	0	0	0	0	2	0	1	0	1	0	5	0	1	07	0	0	0	0	1	2	2	0	0	0	1	1	0	1	3	1
multifida	0	0	0	0	0	1	3	0	0	0	0	1	9	0	1	11	3	0	0	1	0	0	0	1	1	1	1	0	0	0	3	0
mutabilis	1	0	0	0	0	1	2	0	0	0	0	0	0	1	1	07	1	1	0	1	0	0	0	1	1	1	1	0	1	1	3	1
neopauciflora	1	0	0	1	1	1	2	0	0	0	0	0	0	2	0	05	3	0	0	2	0	2	2	0	0	0	0	0	0	0	2	0
nudicaulis	1	0	0	0	0	1	3	1	0	0	0	0	5	0	1	07	2	0	0	1	0	0	0	1	1	1	1	0	0	1	3	1
oliveea	0	0	0	0	1	1	3	0	1	1	1	0	3	0	1	07	3	1	0	2	1	2	2	0	0	0	0	1	0	0	2	0

TABLE 2. Continued.

Taxon	Characters																															
	0 1	0 2	0 3	0 4	0 5	0 6	0 7	0 8	0 9	1 0	1 1	1 2	1 3	1 4	1 5	1 6	1 7	1 8	1 9	2 0	2 1	2 2	2 3	2 4	2 5	2 6	2 7	2 8	2 9	3 0	3 1	3 2
ortegae	0	0	0	1	1	1	2	0	1	0	1	0	0	1	1	05	0	1	0	2	0	2	2	0	0	0	0	0	1	0	3	0
pachypoda	2	1	0	0	0	1	3	0	1	0	1	0	5	0	1	07	2	0	0	1	0	0	0	1	1	1	1	0	1	1	3	1
pauciflora	1	0	0	0	0	0	0	0	0	0	0	0	3	1	1	07	0	0	0	1	0	0	0	0	0	1	0	0	0	1	3	1
peiranoi	2	1	0	0	0	1	3	0	1	0	1	0	5	0	1	07	2	0	1	0	0	2	2	0	0	0	1	0	1	1	3	1
platyphylla	0	0	0	1	0	0	3	1	0	0	0	0	0	0	1	09	0	0	0	2	1	2	2	0	0	0	1	1	0	1	3	0
podagrica	2	0	0	0	0	1	3	1	0	0	0	0	3	0	1	09	2	0	0	1	0	0	0	1	1	1	1	0	0	1	3	1
pohliana	0	0	0	0	0	1	3	0	0	1	1	0	5	0	1	07	2	1	0	1	0	0	0	1	1	1	0	0	1	1	3	1
pseudocurcas	0	0	0	0	0	0	3	0	0	0	0	0	5	0	1	09	0	1	1	0	1	0	0	1	0	0	0	0	0	0	3	0
purpurea	1	0	0	0	0	0	2	0	1	0	1	0	5	0	1	05	2	0	0	2	0	0	1	1	0	0	1	0	1	1	3	1
ribifolia	1	0	0	0	0	1	3	0	1	0	1	0	3	0	1	07	2	2	1	1	0	0	0	1	1	0	0	0	1	1	3	1
ricinifolia	0	0	0	0	0	0	3	0	0	1	0	0	5	0	1	07	3	0	0	1	0	0	0	1	1	1	0	0	1	1	3	1
riojae	1	0	0	1	1	1	2	0	1	0	0	0	0	1	1	05	0	0	0	2	0	2	2	0	0	0	0	0	0	0	3	0
rufescens	0	0	1	1	0	0	3	0	0	0	0	0	0	0	1	09	0	1	0	0	1	0	2	0	0	0	0	1	0	0	3	0
rzedowskii	1	0	0	1	1	1	0	0	0	0	0	0	0	0	1	0	03	0	1	0	2	0	0	0	0	0	0	0	0	0	1	0
standleyi	0	0	0	1	1	1	2	0	1	0	0	0	0	1	1	07	0	0	0	2	1	2	2	0	0	0	0	0	0	0	2	0
stevensii	1	0	0	0	1	1	1	0	0	0	0	0	0	0	1	05	0	1	1	2	1	2	2	0	0	0	0	0	0	1	3	1
sympetala	0	0	0	1	1	1	1	0	0	0	0	0	0	1	1	07	0	0	0	2	1	2	2	0	0	0	0	0	0	0	2	0
tlalcozotitlanensis	1	0	0	0	1	1	3	0	1	0	1	0	0	1	1	05	0	1	0	2	1	2	2	0	0	0	0	1	0	1	3	1
thyrsantha	1	0	0	0	0	1	3	0	1	0	1	0	3	0	1	07	2	2	1	0	1	0	0	1	1	0	0	0	1	1	3	1
tupifolia	1	0	0	0	0	0	3	0	1	1	0	0	3	0	1	07	3	0	0	1	0	1	1	0	0	0	0	0	0	1	3	1
vernicosa	1	0	0	1	1	1	2	0	1	0	1	0	0	1	1	07	2	0	0	2	0	0	0	0	0	0	1	1	1	0	2	0
weddelliana	1	0	0	0	0	1	2	0	0	0	0	0	5	0	1	07	0	0	0	1	0	0	0	1	1	1	1	0	0	1	3	1
yucatanensis	0	0	0	0	0	0	3	0	0	0	0	0	0	0	1	09	0	0	1	0	1	0	2	1	0	0	0	0	0	0	3	0

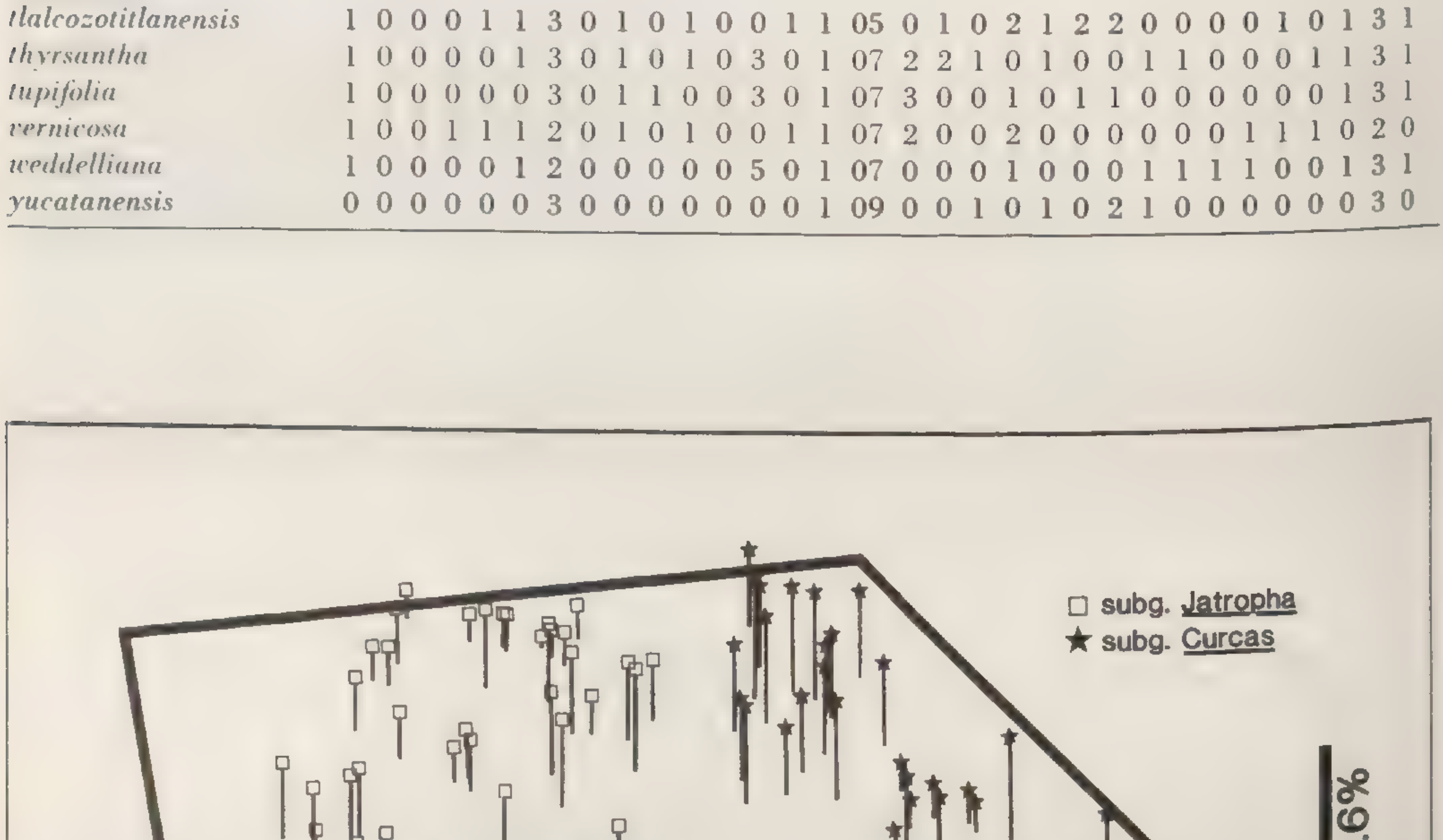

FIGURE 1. PCA of 77 *Jatropha* species from 32 characters, using F. J. Rohlf's NTSYS-pc program. Infrageneric designations are from Dehgan & Webster (1979).

TABLE 3A. Selected characters* with highest factor loadings (in order of magnitude) for each principal component in analysis of 77 species of *Jatropha*.

PC1		PC2		PC3	
Character number	Factor loading	Character number	Factor loading	Character number	Factor loading
4	−0.278	16	−0.327	19	0.384
5	−0.263	6	0.317	26	−0.351
32	0.259	1	0.307	18	0.327
23	−0.256	15	−0.304	9	0.283
25	0.259	14	0.287	20	−0.257
30	0.252	13	−0.204	11	0.274

* See Table 1.

acters are listed in Table 4, and the data matrix is presented in Table 5. Earlier runs were made using PAUP Version 2.4.1 (David Swofford, Illinois Natural History Survey, 1984) and CLADOS Version 0.9 (Kevin Nixon, Bailey Hortorium, Cornell University, 1988). However, these programs both proved unsatisfactory because of limitations on number of taxa or on character coding.

Three sets of analyses were performed, the first using only *Aleurites* G. Forster as an outgroup, the second using only *Joannesia* Vell., and the third with both genera selected as outgroups. Selection of these outgroups was based on (1) the presumed close affinity of *Joannesia* with *Jatropha* in tribe *Joannesiae* (Muell. Arg.) Pax (Webster, 1975, 1994, this issue) and (2) the fact that we consider *Aleurites* to be closely related to *Jatropha* on morphological grounds. We know of no prior discussion of possible sister taxa to *Jatropha*. *Cnidoscolus* Pohl had already been ruled out as a possible sister group (McVaugh, 1944; Miller & Webster, 1962).

Character polarities were not explicitly designated (nonadditive option of Hennig86), but the selection of *Aleurites* and *Joannesia* as outgroups effectively polarized the characters (Maddison et al., 1984; Watrous & Wheeler, 1981). Within each outgroup selection, two algorithms were used

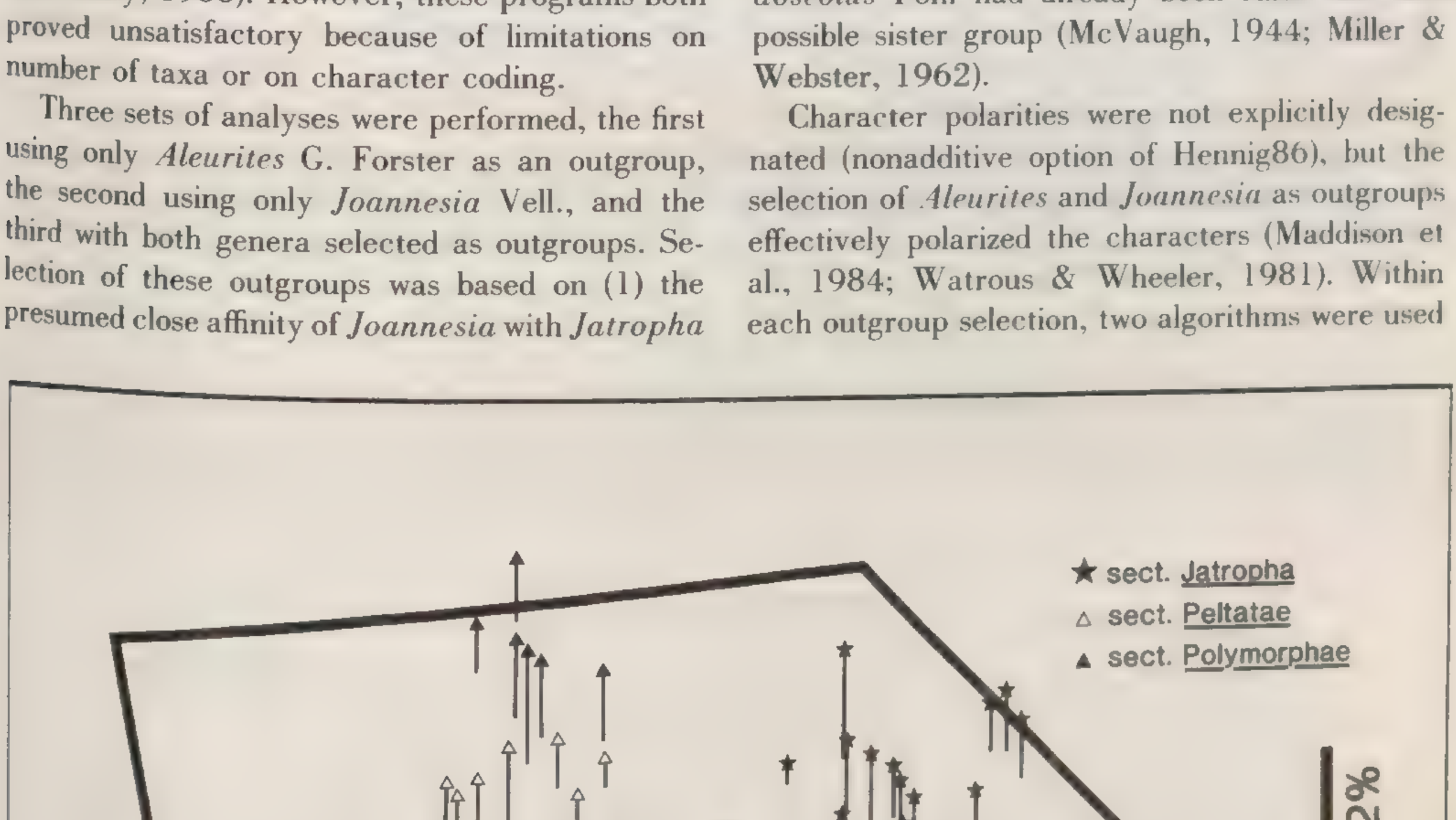

FIGURE 2. PCA of species in *Jatropha* subg. *Jatropha* (including species of sect. *Polymorphae*) from 32 characters, using F. J. Rohlf's NTSYS-pc program. Infrageneric designations are from Dehgan & Webster (1979).

TABLE 3B. Selected characters* with highest factor loadings (in order of magnitude) for each principal component in analysis of 39 species of subgenus *Curcas* with four species of section *Polymorphae*.

PC1		PC2		PC3	
Character number	Factor loading	Character number	Factor loading	Character number	Factor loading
5	−0.337	32	−0.408	9	0.428
6	−0.333	30	0.373	11	0.415
16	0.329	4	0.328	27	0.286
31	0.296	7	0.295	30	0.273
20	−0.279	28	0.273	15	0.260
14	0.272	26	−0.203	19	−0.243

* Characters 2 and 12 were invariant (see Table 1).

to produce cladograms. The first of these is mentioned by Platnick (1989) in his recent comparison of phylogenetic analysis programs, but is not discussed in the program documentation itself. The data matrix is read in with "xread." Subsequently the "treed" option, usually used to supply a user tree, is summoned without an input tree and passed to the branch-breaking algorithm, "bb," which performs extensive branch rearrangement to find more parsimonious trees. This causes the branch-breaker to start with a completely unresolved "bush" (one polytomy consisting of all the EUs). In the second algorithm, the "mhennig*" option is used to supply the initial tree to the branch-breaker, which then attempts to find parsimonious trees. Also, a representative cladogram from each of the PAUP and CLADOS analyses was input by the "treed" option to Hennig86 and subjected to the "m*; bb;" and "tr; bb;" command sequences to ascertain whether Hennig86 could find more parsimonious cladograms by starting with output trees from another program.

RESULTS AND DISCUSSION

The CLADOS, PAUP, and Hennig86 data sets consisted of different numbers of characters (46 binary in CLADOS, 31 multistate in Hennig86 and

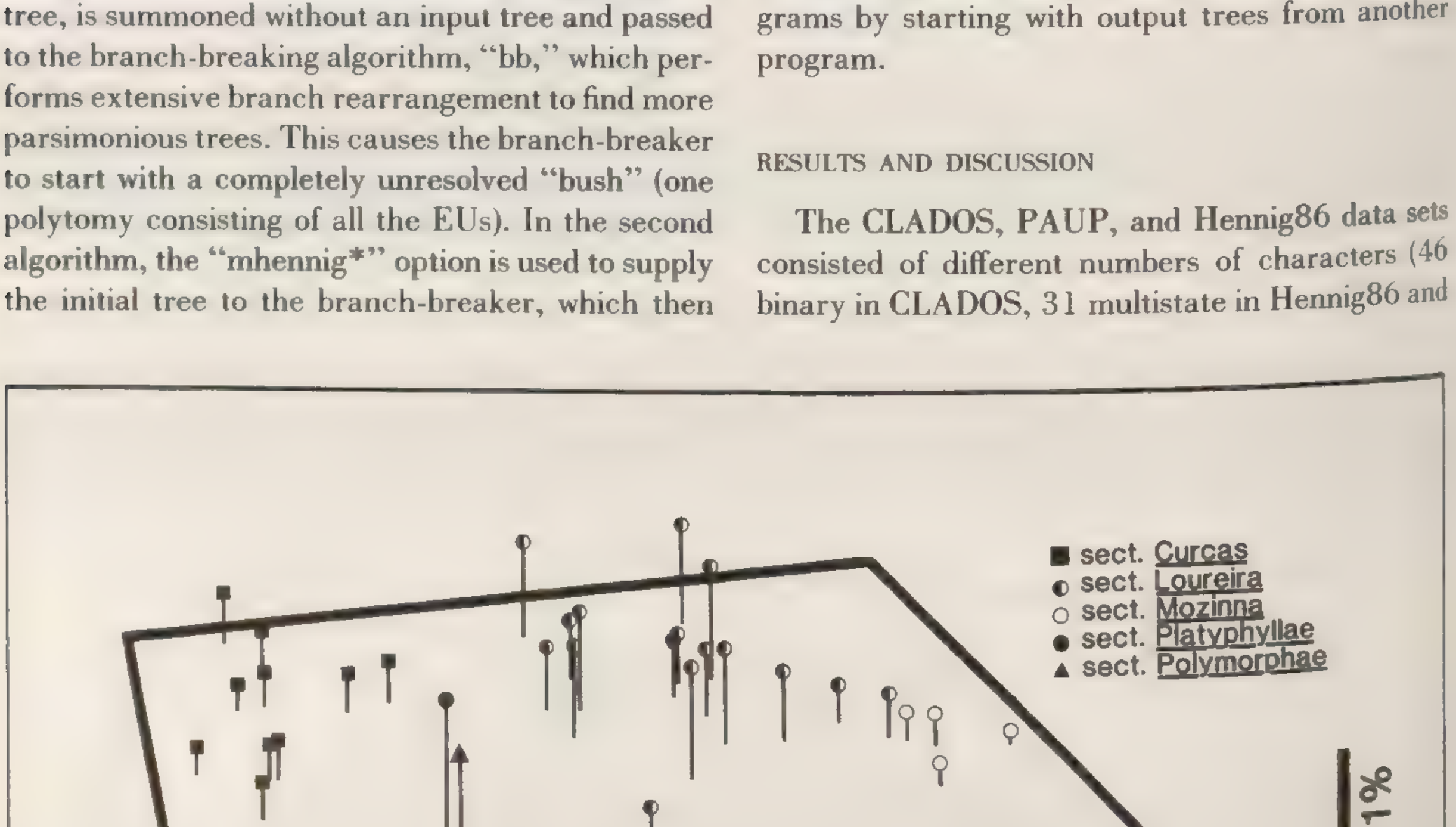

FIGURE 3. PCA of species of *Jatropha* subg. *Curcas* and species of section *Polymorphae* from 32 characters, using F. J. Rohlf's NTSYS-pc program. Infrageneric designations are from Dehgan & Webster (1979).

TABLE 3C. Selected characters* with highest factor loadings (in order of magnitude) for each principal component in analysis of 34 species of subgenus *Jatropha* with four species of section *Polymorphae*.

PC1		PC2		PC3	
Character number	Factor loading	Character number	Factor loading	Character number	Factor loading
19	0.356	7	0.368	12	0.364
18	0.327	25	0.309	23	0.344
9	0.309	6	0.286	24	−0.312
11	0.305	16	0.258	22	0.284
20	−0.298	23	−0.254	8	−0.275
29	0.268	17	0.240	13	0.253

* Characters 3, 4, and 28 were invariant (see Table 1).

PAUP), and taxa (79 in CLADOS and Hennig86, subsets of 4 to 19 taxa in PAUP). Since the consistency index (CI) is highly negatively correlated to the number of taxa and characters in a study, as has been discussed by Archie (1989), we could not compare cladograms by the number of steps or by the CI. Farris himself (1989) admitted that the consistency index (Kluge & Farris, 1969) needed improvement. In order to compare parsimonious cladograms of CLADOS and PAUP to those of Hennig86, we used the "treed" option in Hennig86 to bring one each of the most parsimonious CLADOS and PAUP trees into the program. The "xsteps I" option was then used to calculate the length of

TABLE 4. Characters and character states for cladistic analysis (31 characters numbered 0–30 using the convention of the Hennig86 program).

0. Growth habit:	Plants geophytes (1), plants typical (0).
1. Growth habit:	Plants rhizomatous (1), plants typical (0).
2. Plant sex:	Dioecious (1), monoecious (0).
3. Laticifers:	Articulated and/or nonarticulated (1), idioblastic (0).
4. Laticifers:	Nonarticulated (1), articulated (0).
5. Leaf base:	Peltate (1), not peltate (0).
6. Leaf basal glands:	Present (1), absent (0).
7. Leaf margins:	Toothed (1), entire (0).
8. Leaf marginal glands:	Ciliate-glandular (1), eglandular (0).
9. Leaf sinus depth:	Parted (1), not parted (0).
10. Leaf lobe numbers:	Unlobed (0), 3- (3); 5- (5); 7- (7); 9-lobed (9).
11. Leaf veins:	Palmate (1), pinnate (0).
12. Petioles:	Long (1), subsessile (0).
13. Petiolar traces:	3 (3), 5 (5), 7 (7), 9 (9), 11 (1).
14. Hairs:	Absent (0), unicellular (1), uniseriate-multicellular (2).
15. Coflorescences:	Present (1), absent (0).
16. Flower shape:	Campanulate (0), rotate (1), tubular or urceolate (2).
17. Flower color:	White (1), other (0).
18. Petals of female flowers:	Distinct (0), imbricate (1), connate (2).
19. Petals of male flowers:	Distinct (0), imbricate (1), connate (2).
20. Stamen arrangement:	Monadelphous (1), diadelphous (0).
21. Stamen number:	8 (1), 10 (0).
22. Stamen fusion:	Free (1), connate (0).
23. Style fusion:	Free (1), connate (0).
24. Calyx lobes of female flowers:	Foliaceous (1), not foliaceous (0).
25. Calyx lobe margins:	Glandular (1), entire (0).
26. Fruit dehiscence:	Violently dehiscent (1), tardily dehiscent (0).
27. Fruit locules:	1 (1), 2 (2), 3 (3).
28. Seed:	Carunculate (1), ecarunculate (0).
29. Calyx lobes:	Valvate (1), not valvate (0).
30. Petiolar basal glands:	Present (1), absent (0).

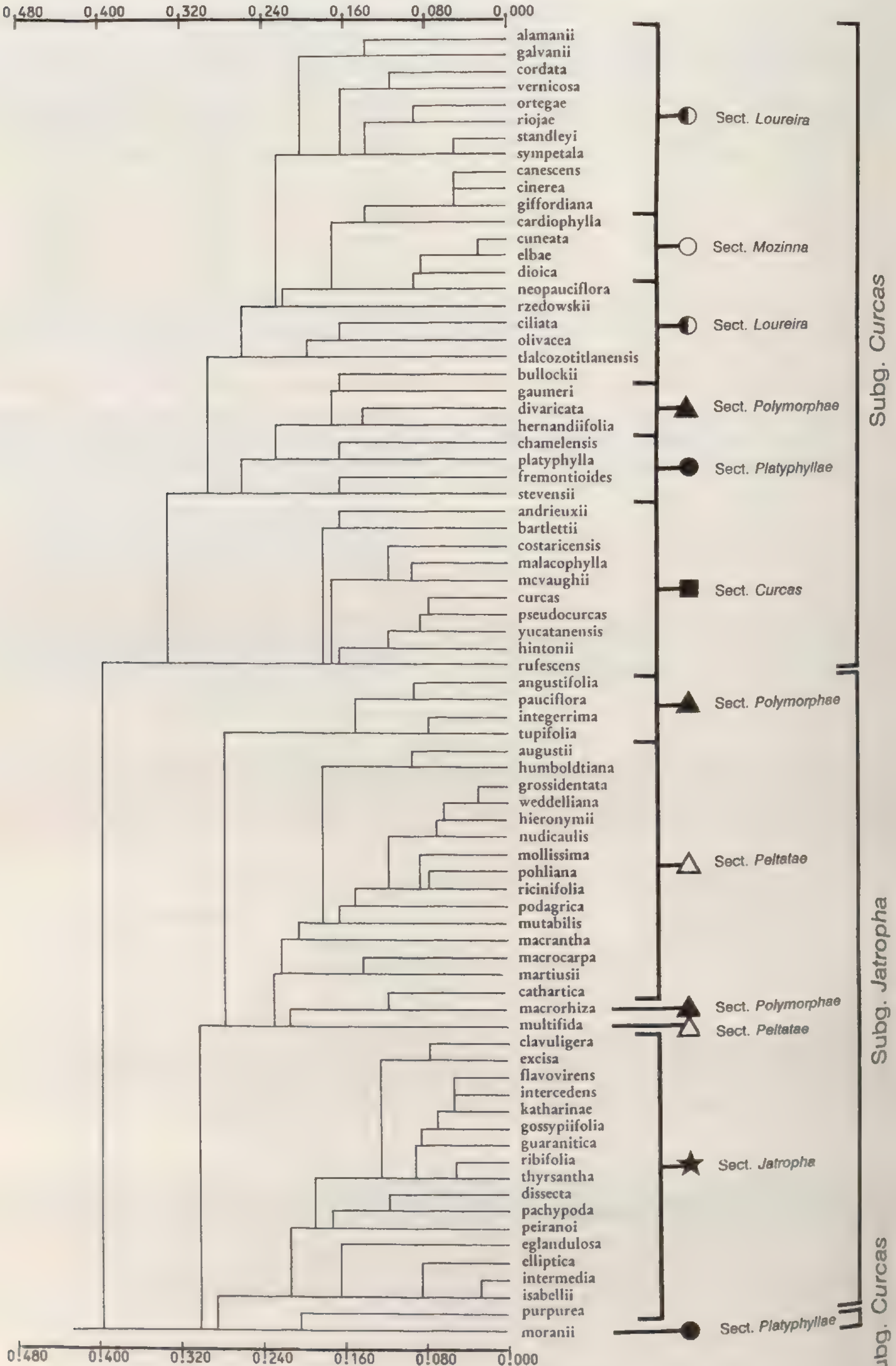

FIGURE 4. Phenogram of 77 Neotropical *Jatropha* species from 32 characters, using F. J. Rohlf's NTSYS-pc program. Infrageneric designations are from Dehgan & Webster (1979).

TABLE 5. Matrix of character states for 77 *Jatropha* species and two outgroups used in the Hennig86 program. Missing states are indicated by "?."

Taxon	Characters
	0 0 0 0 0 0 0 0 0 0 1 1 1 1 1 1 1 1 1 1 2 2 2 2 2 2 2 2 2 2 3
	0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0
joannesia	0 0 0 0 ? 0 0 0 0 1 9 1 0 ? 1 0 0 1 0 0 0 1 0 1 0 1 1 3 1 0 1
aleurites	0 0 0 0 ? 0 0 1 0 0 5 0 0 ? ? 0 1 1 0 0 0 2 0 1 0 1 2 3 1 1 1
alamanii	0 0 1 1 0 0 0 0 0 0 5 0 0 7 0 1 2 1 2 0 0 0 0 0 1 1 1 3 1 0 0
andrieuxii	0 0 1 0 1 0 0 1 0 0 7 0 0 9 1 0 0 1 2 0 0 0 0 0 0 1 1 3 1 0 0
angustifolia	0 0 0 0 1 0 0 0 0 0 1 1 0 7 0 1 1 1 1 1 0 0 0 0 0 1 0 3 0 0 0
augustii	0 0 0 1 0 1 1 0 1 0 5 0 0 7 0 1 1 1 0 0 1 1 0 0 0 1 0 3 0 0 0
bartlettii	0 0 1 0 1 0 0 1 0 0 5 0 0 9 1 0 0 0 0 1 0 0 0 0 1 0 1 3 1 0 0
bullockii	0 0 0 0 1 0 0 0 0 0 3 0 0 5 0 1 2 0 2 0 0 1 0 0 0 1 0 3 0 0 0
canescens	0 0 1 1 0 0 0 0 0 0 1 0 0 5 1 1 2 1 2 2 0 0 0 0 1 1 1 2 1 0 0
cardiophylla	0 1 1 1 0 0 0 0 0 0 1 0 0 5 0 1 2 1 2 2 0 0 0 0 0 1 1 1 1 0 0
cathartica	1 0 0 0 1 0 0 0 0 1 7 0 0 9 0 1 1 1 0 0 1 1 1 1 0 1 0 3 0 0 0
chamelensis	0 0 1 1 0 0 1 0 0 0 1 0 0 9 0 1 2 0 0 2 0 0 0 0 1 1 0 3 1 0 0
ciliata	0 0 1 1 0 0 1 1 1 0 5 0 0 7 0 1 2 0 2 2 0 0 0 0 0 1 0 3 1 0 0
cinerea	0 0 1 1 0 0 0 0 0 0 3 0 0 5 1 1 2 1 2 2 0 0 0 0 1 1 1 2 1 0 0
clavuligera	0 0 0 0 0 0 1 0 1 1 7 0 0 7 2 0 0 1 0 0 0 0 0 1 0 0 0 3 0 0 0
cordata	0 0 1 1 0 0 1 0 1 0 1 1 0 7 0 1 2 1 2 2 0 0 0 0 1 0 1 2 1 0 0
costaricensis	0 0 1 0 1 0 0 0 0 0 5 0 0 7 1 0 2 0 2 2 1 0 0 0 1 1 1 3 1 0 0
cuneata	0 0 1 1 0 0 0 0 0 0 3 2 1 3 0 1 2 0 2 2 0 0 0 0 0 1 1 1 1 0 0
curcas	0 0 0 0 1 0 0 0 0 0 5 0 0 9 0 0 0 0 0 2 0 0 0 0 0 1 1 3 1 0 0
dioica	0 1 1 1 0 0 0 0 0 0 3 2 1 3 0 1 2 1 2 2 0 0 0 0 0 1 1 1 1 0 0
dissecta	1 0 0 0 0 0 1 0 1 1 5 0 0 7 2 0 1 1 0 0 1 1 0 1 0 0 0 3 0 0 0
divaricata	0 0 0 0 0 0 0 0 0 0 1 1 0 7 0 1 2 0 0 0 0 0 0 0 0 1 0 3 0 0 0
eglandulosa	0 0 0 0 0 0 0 0 0 0 1 1 1 7 2 0 0 1 0 0 1 1 1 0 0 1 0 3 0 0 0
elbae	0 0 1 1 0 0 0 0 0 0 1 2 1 3 0 1 2 0 2 2 0 0 0 0 0 1 1 1 1 0 0
elliptica	1 0 0 0 0 0 1 0 1 0 1 1 1 7 2 0 0 1 2 0 1 1 0 0 0 0 0 3 0 0 0
excisa	0 0 0 0 0 0 1 0 1 0 5 0 0 7 1 0 0 1 0 0 0 0 0 1 0 0 0 3 0 0 0
flavovirens	0 0 0 0 0 0 1 0 1 1 3 0 0 7 2 0 0 1 0 0 0 1 0 1 0 0 0 3 0 0 0
fremontioides	0 0 0 1 0 0 0 0 0 0 3 0 1 5 1 1 2 1 2 0 0 0 0 0 0 1 0 3 0 0 0
galvanii	0 0 1 1 0 0 0 0 0 0 1 0 0 7 0 1 0 1 0 0 0 0 0 0 1 0 1 2 1 0 0
gaumeri	0 0 0 0 1 0 0 0 0 0 1 0 0 7 0 1 2 0 2 2 1 1 0 1 0 1 0 3 0 0 0
giffordiana	0 0 1 1 0 0 0 0 0 0 1 0 0 5 1 1 2 1 2 2 0 0 0 0 1 1 1 3 1 0 0
gossypiifolia	0 0 0 0 0 0 1 0 1 0 5 0 0 7 2 0 0 1 0 0 0 1 0 0 0 0 0 3 0 0 0
grossidentata	0 0 0 0 0 0 0 1 0 0 5 0 0 7 0 1 1 1 0 0 1 1 1 1 0 1 0 3 0 0 0
guaranitica	1 0 0 0 0 0 1 0 1 0 3 0 0 7 2 0 0 1 0 0 0 1 0 1 0 0 0 3 0 0 0
hernandiifolia	0 0 0 1 1 0 0 0 0 3 0 0 7 0 1 2 0 1 2 0 0 0 0 0 1 0 3 0 0 0
hieronymii	0 0 0 0 0 0 0 1 0 0 5 0 0 7 0 1 1 1 0 0 1 1 1 1 0 1 0 3 0 0 0
hintonii	0 0 0 0 1 0 0 0 0 0 3 0 0 9 1 0 0 0 0 1 0 0 0 0 0 1 1 3 0 0 0
humboldtiana	0 0 0 0 0 1 1 0 1 0 1 0 0 7 0 1 1 1 0 0 1 1 1 0 0 1 0 3 0 0 0
integerrima	0 0 0 0 1 0 0 0 0 0 3 0 0 7 0 1 1 1 1 1 0 0 0 0 0 1 0 3 0 0 0
intercedens	0 0 0 0 0 0 1 0 1 0 3 0 0 7 2 0 0 1 0 0 0 1 0 0 0 0 0 3 0 0 0
intermedia	1 0 0 0 0 0 1 0 1 0 1 1 1 7 2 0 0 1 0 0 0 1 0 1 0 0 0 3 0 0 0
isabellii	1 0 0 0 0 0 1 0 1 0 1 1 1 7 2 0 0 1 0 0 0 0 0 1 0 0 0 3 0 0 0
katharinae	0 0 0 0 0 0 1 0 1 0 3 0 0 7 2 0 0 1 0 0 0 1 0 1 0 0 0 3 0 0 0
macrantha	0 0 0 0 0 0 0 0 0 0 3 0 0 7 0 1 1 1 0 0 1 0 0 0 0 1 0 1 0 0 0
macrocarpa	0 0 0 0 0 0 0 0 0 1 5 0 0 7 0 1 1 1 0 0 0 1 0 1 0 1 0 3 0 0 0
macrorhiza	1 0 0 0 0 0 0 1 0 1 7 0 0 7 0 1 1 1 0 0 0 1 0 1 0 1 0 3 0 0 0
malacophylla	0 0 1 0 1 0 0 1 0 0 5 0 0 9 1 1 0 0 2 2 1 0 0 0 1 1 1 3 1 0 0
martiusii	0 0 0 0 0 0 0 0 0 1 5 0 0 7 0 1 2 1 2 2 0 1 0 1 0 0 0 3 0 0 0
mcvaughii	0 0 1 0 1 0 0 0 0 0 7 0 0 9 1 0 0 0 2 2 1 0 0 0 0 1 1 3 1 0 0
mollissima	0 0 0 0 0 0 0 0 0 0 5 0 0 7 1 1 1 1 0 0 1 1 1 1 0 0 0 3 0 0 0
moranii	0 0 0 0 1 0 1 0 1 0 5 0 0 7 0 1 0 0 2 2 0 0 0 1 1 1 0 3 0 0 0
multifida	0 0 0 0 0 0 0 0 0 1 9 0 0 1 0 1 1 1 0 0 1 1 1 1 0 1 1 3 1 0 0
mutabilis	0 0 0 0 0 0 0 0 0 0 1 1 0 7 1 1 1 1 0 0 1 1 1 1 0 0 0 3 0 0 0
neopauciflora	0 0 1 1 0 0 0 0 0 0 1 2 1 5 0 1 2 1 2 2 0 0 0 0 0 1 1 2 1 0 0

TABLE 5. Continued.

Taxon	Characters																														
	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	2	3
	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0
nudicaulis	0	0	0	0	0	1	0	0	0	0	5	0	0	7	0	1	1	1	0	0	1	1	1	1	0	1	0	3	0	0	0
olivacea	0	0	0	1	0	0	1	1	1	0	3	0	0	7	1	1	2	0	2	2	0	0	0	0	1	1	1	2	1	0	0
ortegae	0	0	1	1	0	0	1	0	1	0	1	1	0	5	1	1	2	1	2	2	0	0	0	0	0	0	1	3	1	0	0
pachypoda	1	0	0	0	0	0	1	0	1	0	5	0	0	7	0	1	1	1	0	0	1	1	1	1	0	0	0	3	0	0	0
pauciflora	0	0	0	0	1	0	0	0	0	0	3	1	0	7	0	1	1	1	0	0	0	0	1	0	0	1	0	3	0	0	0
peiranoi	1	0	0	0	0	0	1	0	1	0	5	0	0	7	0	0	0	1	2	2	0	0	0	1	0	0	0	3	0	0	0
platyphylla	0	0	1	0	1	1	0	0	0	0	1	0	0	9	0	1	2	0	2	2	0	0	0	1	1	1	0	3	1	0	0
podagrica	0	0	0	0	0	1	0	0	0	0	3	0	0	9	0	1	1	1	0	0	1	1	1	1	0	1	0	3	0	0	0
pohliana	0	0	0	0	0	0	0	1	1	0	5	0	0	7	1	1	1	1	0	0	1	1	1	0	0	0	0	3	0	0	0
pseudocurcas	0	0	0	0	1	0	0	0	0	0	5	0	0	9	1	0	0	0	0	0	1	0	0	0	0	1	1	3	1	0	0
purpurea	0	0	0	0	1	0	1	0	1	0	5	0	0	5	0	1	2	1	0	1	1	0	0	1	0	0	0	3	0	0	0
ribifolia	0	0	0	0	0	0	1	0	1	0	3	0	0	7	2	0	1	1	0	0	1	1	0	0	0	0	0	3	0	0	0
ricinifolia	0	0	0	0	1	0	0	1	0	0	5	0	0	7	0	1	1	1	0	0	1	1	1	0	0	0	0	3	0	0	0
riojae	0	0	1	1	0	0	1	0	0	0	1	1	0	5	0	1	2	1	2	2	0	0	0	0	0	1	1	3	1	0	0
rufescens	0	1	1	0	1	0	0	0	0	0	1	0	0	9	1	1	0	0	0	2	0	0	0	0	1	1	1	3	1	0	0
rzedowskii	0	0	1	1	0	0	0	0	0	0	1	1	1	3	1	1	2	1	0	0	0	0	0	0	0	1	1	1	1	0	0
standleyi	0	0	1	1	0	0	1	0	0	0	1	1	0	7	0	1	2	0	2	2	0	0	0	0	0	1	1	2	1	0	0
stevensii	0	0	0	1	0	0	0	0	0	0	1	0	0	5	1	0	2	0	2	2	0	0	0	0	0	1	0	3	0	0	0
sympetala	0	0	1	1	0	0	0	0	0	0	1	1	0	7	0	1	2	0	2	2	0	0	0	0	0	1	1	2	1	0	0
tlalcozotitlanensis	0	0	0	1	0	0	1	0	1	0	1	1	0	5	1	1	2	0	2	2	0	0	0	0	1	1	0	3	0	0	0
thyrsantha	0	0	0	0	0	0	1	0	1	0	3	0	0	7	2	0	0	0	0	0	1	1	0	0	0	0	0	3	0	0	0
tupifolia	0	0	0	0	1	0	1	1	0	0	3	0	0	7	0	1	1	1	1	1	0	0	0	0	0	1	0	3	0	0	0
vernicosa	0	0	1	1	0	0	1	0	1	0	1	1	0	7	0	1	2	1	0	0	0	0	0	1	1	0	1	2	1	0	0
weddelliana	0	0	0	0	0	0	0	0	0	0	5	0	0	7	0	1	1	1	0	0	1	1	1	1	0	1	0	3	0	0	0
yucatanensis	0	0	0	0	1	0	0	0	0	0	1	0	0	9	0	0	0	0	0	2	1	0	0	0	0	1	1	3	1	0	0

the trees relative to the Hennig86 data set. The shortest CLADOS and PAUP trees evaluated to 263 and 269 steps, respectively. The Hennig86 program, however, produced in excess of 100 equally parsimonious trees, all 230 steps long, when a data set with two outgroups was used. The trees from all data sets with one outgroup had a greater number of steps. The cladogram in Figure 5 was selected by calculating character weights ("xsteps w" command) and applying them to all 100+ cladograms. The program arrives at weights based upon the CI and retention index (RI) of the cladograms considered. The lengths of the cladograms were recalculated using weighted characters ("xsteps l" command). The shortest one is illustrated in Figure 5. The trees were calculated using all available unweighted data, but the one selected gives more credence to characters showing less homoplasy, without resorting to a successive approximations approach, such as that suggested by Carpenter (1988). Even prior to Archie's (1989) criticism of the consistency index, Farris had already abandoned it in his 1988 release of Hennig86 in favor of two new indices: the Retention Index (RI) and the Rescaled Consistency Index (RC). These are constructed to behave as true indices, possessing values between 0 and 1 (Farris, 1989). The most parsimonious cladograms from Hennig86 all had RC = 0.19 and RI = 0.72. Stated simply, RC displays a high degree of homoplasy in the data set, while the high value for RI shows that these cladograms exhibit a relatively low degree of homoplasy as compared to the total amount possible for the data set.

The strict (Nelson) consensus cladogram (Fig. 5) output by Hennig86 is remarkably similar to Dehgan & Webster's (1979) evolutionary model, which utilized morphological similarities and dif-

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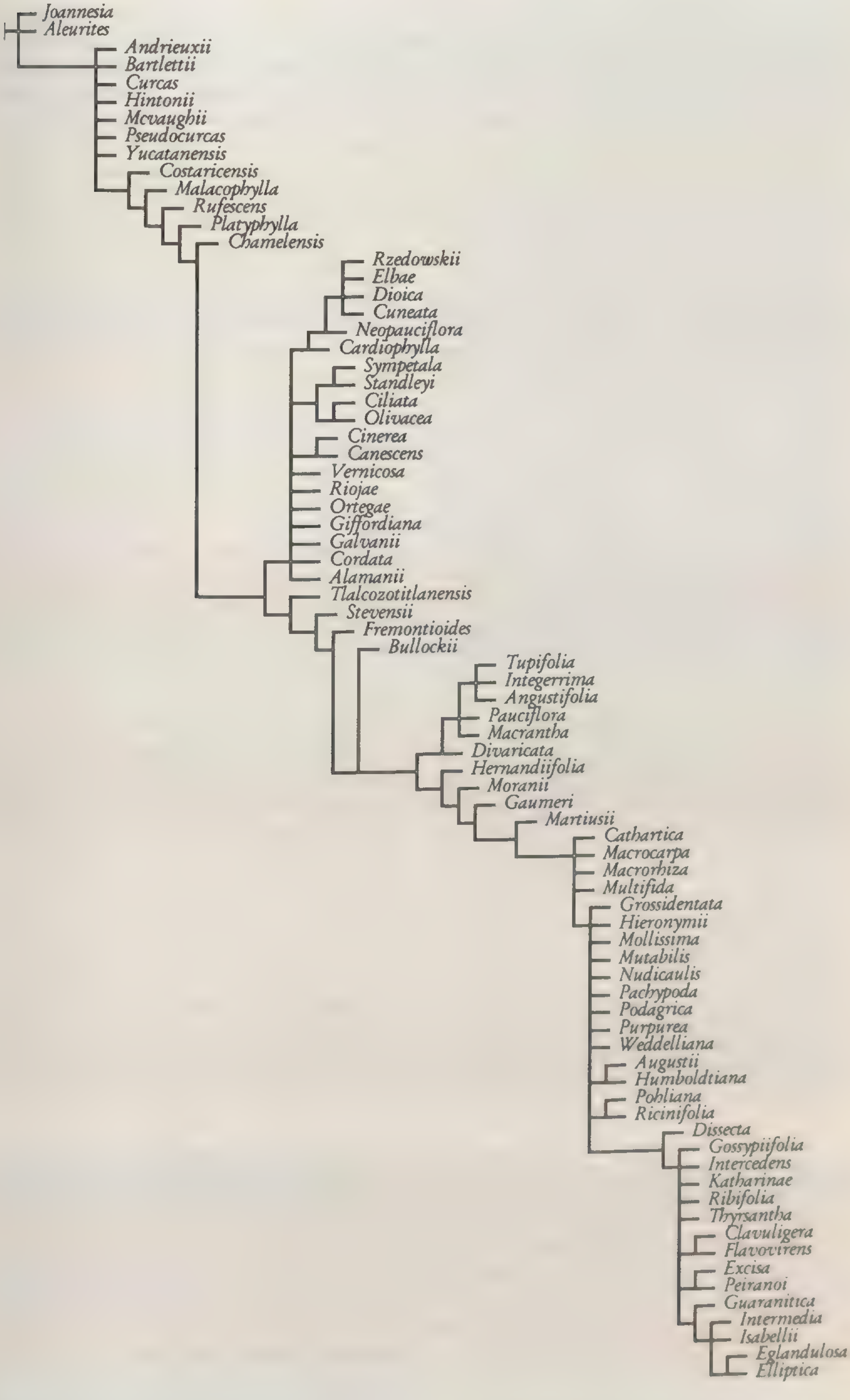
FIGURE 5. Nelson (strict) consensus tree for 77 *Jatropha* species and two outgroups (*Joannesia* and *Aleurites*) derived from analysis of 31 unweighted and unordered morphological characters (cf. Table 4), using Farris's Hennig86 program.


Joannesia
Aleurites
Andrieuxii
Bartlettii
Curcas
Hintonii
Mcvaughii
Pseudocurcas
Yucatanensis
Costaricensis
Malacophylla
Rufescens
Platyphylla
Chamelensis
Rzedowskii
Elbae
Dioica
Cuneata
Neopauciflora
Cardiophylla
Sympetala
Standleyi
Ciliata
Olivacea
Cinerea
Canescens
Vernicosa
Riojae
Ortegae
Giffordiana
Galvanii
Cordata
Alamanii
Tlalcozotitlanensis
Stevensii
Fremontioides
Bullockii
Tupifolia
Integerrima
Angustifolia
Pauciflora
Macrantha
Divaricata
Hernandiifolia
Moranii
Gaumeri
Martiusii
Cathartica
Macrocarpa
Macrorhiza
Multifida
Grossidentata
Hieronymii
Mollissima
Mutabilis
Nudicaulis
Pachypoda
Podagrica
Purpurea
Weddelliana
Augustii
Humboldtiana
Pohliana
Ricinifolia
Dissecta
Gossypiifolia
Intercedens
Katharinae
Ribifolia
Thyrsantha
Clavuligera
Flavovirens
Excisa
Peiranoi
Guaranitica
Intermedia
Isabellii
Eglandulosa
Elliptica

ferences in concert with the principles of evolutionary reduction series. The classification of Dehgan & Webster (1979) is consistent with a convex interpretation of the most parsimonious Hennig86 cladogram. Use of convex groups in systematics, though debatable, has been advocated by many, including Ashlock (1971), Cronquist (1987), Meacham & Duncan (1987), and others. Although delimitations of the sections and subsections are subject to individual interpretation and some minor realignment of taxa within groups is advisable, the fundamental infrageneric relationships remain mostly intact. Subgenus *Jatropha* as a whole is shown to be monophyletic, whereas subgenus *Curcas* and some of its species groups are paraphyletic.

The strict (Nelson) consensus tree (Fig. 5) clearly indicates the relationship between the two subgenera. In particular, early derivation and basal position of subgenus *Curcas* closely corresponds to the previously suggested arrangement. The consensus cladogram (Fig. 5) would support reduction of sections *Platyphyllae* and *Mozinna* to subsections of the more heterogeneous section *Loureira*. *Mozinna*, which initially included only three species, was recognized as a distinct section based on unilocular fruit with a single seed, rhizomatous growth habit, and tetraploid (in *J. cuneata* Wiggins & Rollins and *J. dioica*) or unusually large (in *J. cardiophylla* (Torr.) Muell. Arg.) chromosomes. Recent discovery of two new species (*J. elbae* J. Jiménez Ramírez and *J. rzedowskii* J. Jiménez Ramírez) and inclusion of *J. neoplauciflora* Pax (placed in subsect. *Neopauciflorae* Pax of sect. *Loureira* by Dehgan & Webster, 1979), all three with bilocular fruit but with several characteristics similar to those of the three original species, make recognition of the group at sectional level more debatable. Analogous to *Mozinna*, section *Loureira* includes species with bi- and trilocular fruit. In subsection *Canescentes* Pax ex Dehgan & Webster, for example, *J. canescens* (Benth.) Muell. Arg. and *J. cinerea* (Ortega) Muell. Arg. are bilocular, while *J. giffordiana* Dehgan & Webster is mostly trilocular. Although higher locule number in some exceptional cases may be the result of reversal (as in *J. neopauciflora*), in nearly all other cases it is ancestral.

The suggested changes in subgenus *Jatropha* include transfer of *J. moranii*, which was initially placed in section *Platyphyllae* (Dehgan & Webster, 1978) to section *Polymorphae*. This species differs from most members of *Polymorphae* by its glandular leaf margins and possession of foliar sepals in the female flowers. *Jatropha macrorhiza* Benth. (endemic to southern Arizona in the Sonoran Desert), which was recognized as distinct subsection *Macrorhizae* in *Polymorphae*, would be transferred to section *Peltatae*, together with *J. cathartica* Terán & Berland, *J. macrocarpa* Griseb., and *J. multifida* L., with which it shares several characters, all of which would be accommodated in subsection *Multifidae* Pax. *Jatropha macrantha* Muell. Arg. is accurately placed in section *Polymorphae*. *Jatropha purpurea*, *J. martiusii* (a narrow endemic in Bahia, Brazil), and *J. bullockii* have previously been enigmatic. However, the results of cladistic analysis clearly show their phylogenetic position. *Jatropha bullockii* is indicated to be a sister taxon to the clade containing subgenus *Jatropha* with several autapomorphies and also is phenetically distinct. It is the only non-caudiciform Mexican species with eight stamens, trilocular fruit, and carunculate seeds but very small tubular flowers. *Jatropha martiusii* occupies a transitional position between sections *Polymorphae* and *Peltatae*. It shares certain features of both sections, but in fact does not fit properly into either one. It is the only known South American species with distinctly tubular flowers and trilocular fruit but only two (as opposed to three) style branches. No other species in the genus is known to consistently possess a combination of tubular flowers, two style branches, and three locular fruits. *Jatropha purpurea* is morphologically intermediate between sections *Peltatae* and *Jatropha*. It shares extrafloral glands, ten biseriate stamens, and tubular flowers with *J. cordata* (Ortega) Muell. Arg. (sect. *Loureira*), but has red flowers, trilocular fruit, and carunculate seeds similar to those of section *Jatropha*. Two new sections should be erected to accommodate *J. martiusii* and *J. purpurea*. Accordingly, section *Jatropha* would include three subsections: *J. gossypiifolia* and its related taxa, *J. purpurea*, and *J. isabellii* Muell. Arg. and its related caudiciform South American species.

C. Comparisons Between and Ramifications of Phenetic and Cladistic Analyses

There exists a general concordance between groupings suggested by phenetic and cladistic analyses. Where discrepancies exist, these may be mostly attributed to the inability of phenetic analyses to distinguish homoplastic from patristic similarity. Since the *Jatropha* data set exhibited a large degree of homoplasy, some differences between the two were anticipated. In fact, fewer discrepancies were noted than expected. There was general agreement between the two methodologies

with regard to establishment of subgenera, sections, and most subsections. Moreover, correspondence of the results of cladistic and phenetic studies to Dehgan & Webster's (1979) intuitive classification confirms that intimate knowledge of living (as opposed to preserved) organisms is often essential for establishment of phylogenetic relationships. The nearly identical intuitive and numerical results in *Jatropha* are not a coincidence, but rather are the result of recurrent observation of growth and flowering of plants in the wild and in cultivation. The large numbers of evolutionary changes that have resulted in recognizable morphological discontinuities were reflected in the traditional classification, and for the most part, supported by the numerical analyses presented here.

D. Relationships Between Phytogeography, Evolution, and the Results of Numerical Analyses

We are fully cognizant of the shortcomings of performing phenetic and phylogenetic analyses of only the American taxa. To have a better understanding of the entire genus it is imperative that African and Indian species also be included in the study. Accordingly, we have not used this opportunity to construct a new classification of the genus. This would have been largely unnecessary because of the close similarity between these results and those of the previous classification of Dehgan & Webster (1979). Moreover, it is highly unlikely that inclusion of the Old World taxa would profoundly change the results and discussions presented here. Analogous to the neotropical species, complex evolutionary history of the African taxa is illustrated in the recent works of Hemming & Radcliffe-Smith (1987), in which 25 Somalian species are placed in six sections and five subsections (all in sect. *Spinosae* Pax). The limitation of this study to the neotropical species precludes inclusion of the Old World species at this time. However, the large number of neotropical taxa in *Jatropha*, their widespread geography in concert with narrow endemism of a vast majority of the taxa, known cases of natural hybridization, and probability of extinctions, all profoundly influence the results of numerical studies and will be discussed in the monograph of the genus. Suffice it to say that the adaptive radiation in Mexico and South America that Dehgan & Webster (1979) have addressed is also reflected in the consensus tree. Several other evolutionary concepts that were put forth in earlier works (Dehgan, 1980, 1982, 1984; Dehgan & Craig, 1978; Dehgan & Webster, 1978, 1979) have been confirmed. Of particular interest is the evolutionary progression of infrageneric groups.

As evidenced by the cladistic analyses, species of section *Curcas* originated first. Primitiveness of the section, and of *J. curcas* in particular, was noted by McVaugh (1945) and Wilbur (1954), who maintained that the genus must have originated in Mexico because *J. curcas*, the most primitive species, and several closely related taxa occur there. The primitiveness of this taxon was justified by Dehgan & Webster (1979) on morphological grounds and is supported by the results of the present study. The large number and extreme diversity of taxa of subgenus *Curcas* in Mexico may be explained by recent introduction of a taxon similar to *J. curcas* to an ecogeographically dissimilar habitat, followed by progressive mosaic evolution and mosaic selection (Stebbins, 1984). Geological and climatic disturbances in Mexico (Toledo, 1981; Graham, 1987, 1989b) have probably resulted in both elimination of many taxa related to those in South America and relatively rapid mosaic speciation, which resulted in the largest concentration of *Jatropha* species of any region.

In general, speciation of *Jatropha* in the Neotropics has been most rapid in three seasonally dry regions: grassland-savanna (cerrado), thorn forest-scrub, and caatingas vegetation. In South America, species of sections *Jatropha* and *Peltatae* are found in drier areas of northern Argentina, Brazil, Paraguay, Bolivia, Peru, and Colombia, but are completely lacking from the moist Amazon region. Although a vast majority of the species in sections *Curcas*, *Loureira*, and *Mozinna* are Mexican endemics, all other sections are also represented in Mesoamerica, from Costa Rica, Guatemala, Mexico, Baja California, northward to southern Arizona and Texas. Of the comparatively few West Indian species, at least four are endemic to Cuba and one to Jamaica. Since nearly all jatrophas are to a greater or lesser extent dry-adapted succulents, their absence from the wetter regions of South America is understandable. Webster (1994) has suggested that the Euphorbiaceae probably arose in West Gondwanaland, with Africa harboring the greatest diversity of the primitive taxa in the five subfamilies. Dehgan (1980 et seq.) and Dehgan & Craig (1978) enumerated the primitive features of *Jatropha* and suggested its possible ancestral position to the Euphorbiaceae. This view is further supported by Gilbert and others in this issue. As such, jatrophas probably originated and evolved in drier regions of Gondwanaland and never developed the ability to adapt to wet tropical forests (cf. Retallack & Dilcher, 1981).

Despite pantropical distribution of *Jatropha*, a vast majority of its species are endemic and often restricted to small regions. Other than *J. gossypiifolia*, which is reported to be eaten and disseminated by pigeons (Standley, 1923), no cases of long-distance dispersal have been reported, and the present distribution of the genus appears to be the result of progressive overland dispersal. With the exception of a few taxa that have become spontaneous or subspontaneous with the help of humans, no truly disjunct species have been reported within or between the continents of Africa, America, and the subcontinent of India. Their complete absence from all oceanic islands (except *J. divaricata* and *J. hernandiifolia* in Jamaica) is a further indication of their inability to disperse by birds or ocean currents. The large number of narrowly endemic species is indicative of natural habitat disturbance, as has reportedly occurred in Central and South America (Graham, 1989a), and hence agrees with the refugium theory (Prance, 1982). Interestingly, several other genera in the Euphorbiaceae with dehiscent fruit and carunculate seeds, such as *Aleurites* in Asia, *Hevea* Aubl., *Joannesia*, *Cnidoscolus*, *Manihot* Miller, and others in America, and *Grossera* Pax, *Crotonogyne* Muell. Arg., and others in Africa, although widespread within the confines of a single continent, are not dispersable by interoceanic means. Therefore, it is reasonable to assume that disjunct presence of jatrophas in three widely separated regions is a good indication of its antiquity, and hence, its primitiveness.

Reductions and modifications have occurred in conjunction with migration from south to north in Mesoamerica and north to south in South America and are generally associated with increasing aridity and cold. Grant (1963: 566–568) has suggested that speciation may be inextricably involved in some cases of phyletic evolution, where a progression takes place as a series of successive speciational steps. Adaptive gradual speciation (Stebbins, 1984) in *Jatropha* is exhibited in growth habit (from arborescent to rhizomatous or tuberous-caudiciform), inflorescences (terminal compound dichasium with a distinct coflorescence to lateral or terminal solitary flowers), number of stamens (10 to 8) and their arrangement (uni- or biseriate, monadelphous or free), reductions in ovary locule numbers (from 3 to 2 and 1) which, with the notable exception of *J. martiusii* (with 2 styles but 3 locules), is invariably accompanied by reduction from 3- to 2- to 1-bifid, free or connate styles, and plant sexuality (from monoecy to gynodioecy to dioecy). Progressive diversifying selection, as a result of migration and ensuing geographical isolation, was probably followed by a shorter or longer period of directional selection, finally culminating in stabilizing selection at the maximum level of fitness possible for the gene pool (Dobzhansky, 1970; Stebbins, 1974). Since overland migration often involves shifts in environmental and edaphic conditions, a population may respond by evolving in a new direction or by becoming extinct (Stebbins, 1974).

Gradual shifts in response to aridity and/or cold are illustrated in the species of subgenus *Curcas*. Species of southern Mexico are usually monoecious semi-evergreen trees with large to very large leaves, massive terminal inflorescences, female flowers with three bifid stigmas, trilocular fruit, and diploid chromosome numbers. In contrast, extreme northern species of section *Mozinna* are much branched, dioecious, deciduous, rhizomatous subshrubs with short shoots and small to very small leaves, lateral few (♂) or solitary (♀) inflorescences, female flowers with a single bifid stigma, unilocular fruit, and polyploid chromosome numbers. Thus, species of *Jatropha* have endured gradual mosaic evolutionary changes, as reflected in their great diversity of adaptive types, which are inextricably correlated with their geographical distribution.

The above observations are reflected in the results of the phylogenetic analyses. An ancestral taxon similar to *J. Curcas* (sect. *Curcas*) seems to have been the source from which species of sections *Platyphyllae*, *Loureira*, and subsequently *Mozinna* originated in Mesoamerica. Furthermore, section *Curcas* or a taxon with similar features also gave rise to species of section *Polymorphae*, leading the way to evolution of taxa in section *Peltatae*. Section *Jatropha* is shown to have evolved from some portion of section *Peltatae*. Several taxa described after Dehgan & Webster's (1979) publication appear to have been appropriately placed in the phylogenetic scheme. In short, the earlier classification recognized grade taxa based on symplesiomorphic features. Only some minor adjustments to previously recognized phylogenetic groupings will have to be made in the forthcoming monograph of the genus. It is fascinating that while the classification of Dehgan & Webster (1979) is based on phenetic studies, the authors have presented a phylogenetic diagram remarkably similar to the results of cladistic analyses presented herein.

Literature Cited

Adanson, M. 1763. Pp. 346–358 *in* Familles des Plantes XLV. Familles les Titimales. Tithymali.

Archie, J. W. 1989. Homoplasy excess ratios: New indices for measuring levels of homoplasy in phylo-

genetic systematics and a critique of the consistency index. Syst. Zool. 38: 253–269.

ASHLOCK, P. D. 1971. Monophyly and associated terms. Syst. Zool. 20: 63–69.

BAILLON, H. 1858. Etude générale du groupe des Euphorbiacées, pp. 294–296.

CARPENTER, J. M. 1988. Choosing among multiple equally parsimonious cladograms. Cladistics 4: 291–296.

CRONQUIST, A. 1987. A botanical critique of cladism. Bot. Rev. 53: 1–52.

DEHGAN, B. 1980. Application of epidermal morphology to taxonomic delimitations in the genus *Jatropha* L. (Euphorbiaceae). J. Linn. Soc. Bot. 80: 257–278.

———. 1982. Comparative anatomy of the petiole and infrageneric relationships in *Jatropha* (Euphorbiaceae). Amer. J. Bot. 69: 1283–1295.

———. 1984. Phylogenetic significance of interspecific hybridization in *Jatropha* (Euphorbiaceae). Syst. Bot. 9: 467–478.

——— & M. E. CRAIG. 1978. Types of laticifers and crystals in *Jatropha* and their taxonomic implications. Amer. J. Bot. 65: 345–352.

——— & G. L. WEBSTER. 1978. Three new species of *Jatropha* from western Mexico. Madroño 25: 30–39.

——— & ———. 1979. Morphology and infrageneric relationships of the genus *Jatropha* (Euphorbiaceae). Univ. Calif. Publ. Bot. 74: 1–73 + 33 plates.

DOBZHANSKY, T. 1970. Genetics of the Evolutionary Process. Columbia Univ. Press, New York.

FARRIS, J. S. 1989. The retention index and the rescaled consistency index. Cladistics 5: 417–419.

GRAHAM, A. 1987. Tropical American Tertiary floras and paleoenvironments: Mexico, Costa Rica, and Panama. Amer. J. Bot. 74: 1519–1531.

———. 1989a. Late Tertiary paleoaltitudes and vegetational zonation in Mexico and Central America. Acta Bot. Neerl. 38: 417–424.

———. 1989b. Paleofloristic and paleoclimatic changes in the Tertiary of northern Latin America. Rev. Paleobot. Palynol. 60: 283–293.

GRANT, V. 1963. The Origin of Adaptations. Columbia Univ. Press, New York.

HEMMING, C. F. & A. RADCLIFFE-SMITH. 1987. A revision of the Somali species of *Jatropha* (Euphorbiaceae). Kew Bull. 42: 103–122.

KLUGE, A. G. & J. S. FARRIS. 1969. Quantitative phyletics and the evolution of anurans. Syst. Zool. 18: 1–32.

LINNAEUS, C. 1763. Pp. 1428–1430 *in* Species Plantarum, 2nd ed.

MADDISON, W. P., M. J. DONOGHUE & R. MADDISON. 1984. Outgroup analysis and parsimony. Syst. Zool. 33: 83–103.

MCVAUGH, R. 1944. The genus *Cnidoscolus*: Generic limits and intergeneric groups. Bull. Torrey Bot. Club 71: 457–474.

———. 1945. The genus *Jatropha* in America: Principal intergeneric groups. Bull. Torrey Bot. Club 72: 271–294.

MEACHAM, C. A. & T. DUNCAN. 1987. The necessity of convex groups in biological classificaiton. Syst. Bot. 12: 78–90.

MILLER, K. I. & G. L. WEBSTER. 1962. Systematic position of *Cnidoscolus* and *Jatropha*. Brittonia 14: 174–180.

MUELLER ARGOVIENSIS, J. 1874. *Jatropha*. *In:* Martius (editor), Flora Brasiliensis 11(2): 486–502.

OLOWOKUDEJO, J. D. 1993. Comparative epidermal morphology of West African species of *Jatropha* L. (Euphorbiaceae). Bot. J. Linn. Soc. 111: 139–154.

PAX, F. 1910. Euphorbiaceae–Jatropheae. Pp. 1–148 *in* Das Pflanzenreich IV.147 (Heft 42). Verlag von Wilhelm Engelmann, Leipzig.

PLATNICK, N. I. 1989. An empirical comparison of microcomputer parsimony programs, II. Cladistics 5: 145–161.

POHL, J. E. 1827. Plantarum Brasiliae Icones et Descriptiones Vindobonae 1: 12, t. 9.

PRANCE, G. T. 1982. A review of the phytogeographic evidences for pleistocene climate changes in the Neotropics. Ann. Missouri Bot. Gard. 69: 594–624.

RADCLIFFE-SMITH, A. 1987. Euphorbiaceae (part 1). *In:* R. M. Polhill (editor), Flora of East Africa. Published on behalf of the East African Government by A. A. Balkaema, Rotterdam/Boston.

RETALLACK, G. & D. L. DILCHER. 1981. A costal hypothesis for the dispersal and rise to dominance of flowering plants. *In:* K. J. Niklas (editor), Paleobotany, Paleoecology and Evolution, Vol. 2. Praeger Publishers, New York.

SNEATH, P. H. A. & R. R. SOKAL. 1973. Numerical Taxonomy. W. H. Freeman, San Francisco.

STANDLEY, P. 1923. Trees and shrubs of Mexico. Contrib. U.S. Nat'l. Herb. 3: 634–642.

STEBBINS, G. L. 1974. Flowering Plants: Evolution Above the Species Level. The Belknap Press, Cambridge.

———. 1984. Mosaic evolution, mosaic selection and angiosperm phylogeny. Bot. J. Linn. Soc. 88: 149–164.

TOLEDO, V. M. 1981. Pleistocene changes of vegetation in tropical Mexico. *In:* G. T. Prance (editor), Biological Diversification in the Tropics. Colombia Univ. Press, New York.

WATROUS, L. E. & Q. D. WHEELER. 1981. The outgroup comparison method of character analysis. Syst. Zool. 30: 1–11.

WEBSTER, G. L. 1975. Conspectus of a new classification of the Euphorbiaceae. Taxon 24: 593–601.

———. 1987. A new species of *Jatropha* (Euphorbiaceae) from Nicaragua. Ann. Missouri Bot. Gard. 74: 117–120.

———. 1987. The saga of the spurges: A review of classification and relationships in the Euphorbiales. J. Linn. Soc. Bot. 94: 3–46.

———. 1994. Classification of the Euphorbiaceae. Ann. Missouri Bot. Gard. 81: 3–32.

——— & L. J. POVEDA. 1978. A phytogeographically significant new species of *Jatropha* (Euphorbiaceae) from Costa Rica. Brittonia 30: 265–270.

WILBUR, R. L. 1954. A synopsis of *Jatropha*, subsection *Eucurcas*, with the description of two new species from Mexico. J. Elisha Mitchell Sci. Soc. 70: 92–101.

APPENDIX. Specimens representative of the *Jatropha* species examined.

Species and authority	Herbarium	Collector and number	Country
J. alamanii Muell. Arg.	MICH	King 1397	Mexico
J. andrieuxii Muell. Arg.	CAS	Salas 1175	Mexico
J. angustifolia Griseb.	NY	Jennings 147	Cuba
J. augustii Pax & Hoffm.	CAL	Belshaw 3056	Peru
J. bartlettii Wilbur	MICH*	R. L. & C. R. Wilbur 1472	Mexico
J. bullockii E. Lott	MICH	McVaugh 26284	Mexico
J. canescens (Benth.) Muell. Arg.	KEW*	Hinds 1841	Mexico
J. cardiophylla (Torr.) Muell. Arg.	DAV	Dehgan & Webster B74.023	US—Arizona
J. cathartica Terán & Berland	BM	Fryxell 2943	US—Texas
J. chamelensis L. A. Pérez-Jiménez	ENCB, MICH	Rzedowski & McVaugh 1400	Mexico
J. ciliata Sessé	CAS, ENCB, F, GH, M, MIN, MO, NY, UC, US, BM	Pringle 6348	Mexico
J. cinerea (Ortega) Muell. Arg.	RSA, GH, NY	Gentry 7050	Mexico
J. clavuligera Muell. Arg.	GM, GH**, NY**	G. Mandon 1073	Bolivia
J. cordata (Ortega) Muell. Arg.	MICH	McVaugh 22107	Mexico
J. costaricensis Webster & Poveda	DAV*	G. L. Webster & L. J. Poveda 22160	Costa Rica
J. cuneata Wiggins & Rollins	DAV, MICH, NY	Webster & Lynch 17008	Mexico
J. curcas L.	FLAS	Dehgan B86.050	Mexico
J. dioica Sessé	DAV	Dehgan B67.279	Mexico
J. dissecta (Chod. & Hassl.) Pax	GH*, KEW**	Hassler 4333	Paraguay
J. divaricata Swartz	BM	Webster & Wilson 5073	Jamaica
J. eglandulosa Pax	BM*	Hassler 8233	Paraguay
J. elbae J. Jiménez Ramírez	FLAS	Soto 254	Mexico
J. elliptica (Pohl) Muell. Arg.	BM, KEW, MO	Steinbach 6708	Brazil
J. excisa Griseb.	KEW, BM	Venturi 7991	Argentina
J. flavovirens Pax & Hoffm.	KEW*, BM**	Hassler 2489	Paraguay
J. fremontioides Standley	NY**	Fisher 35498	Mexico
J. galvanii J. Jiménez Ramírez	FLAS	Contreras & Jiménez s.n.	Mexico
J. gaumeri Greenman	US, TEX, MICH	Lundell & Lundell 7502	Mexico
J. giffordiana Dehgan & Webster	DAV*	Dehgan B74.019	Mexico
J. gossypiifolia L.	FLAS	Dehgan & Webster BD86.300	Brazil
J. grossidentata Pax and Hoffm.	LPB	Beck 6442	Bolivia
J. guaranitica Speg.	UC*	Hassler 10104	Paraguay
J. hernandiifolia Vent.	KEW	Fuertes 359	Dominican Republic
J. hieronymu O. Ktze.	LPB	Beck 4970	Bolivia
J. hintonii Wilbur	BM*	Hinton 4300	Mexico
J. humboldtiana McVaugh	GH	Weberbauer 6211	Peru
J. integerrima Jacq.	MO, NY, F, GH	Combs 99	Cuba
J. intercedens Pax	MICH*, BM**, B**	Fiebrig 5393, Fiebrig 2158	Bolivia
J. intermedia (Chodat & Hassler) Pax	MICH*	Hassler 3795	Paraguay
J. isabellii Muell. Arg.	BM*	Hassler 4338, 5930	Paraguay
J. katharinae Pax	BM**	E. Hassler 9078	Paraguay
J. macrantha Muell. Arg.	KEW	Sauderman 3983	Peru
J. macrocarpa Griseb.	BM, KEW	Venturi 5472	Argentina
J. macrorhiza Benth.	DAV	Dehgan B74.076	US—Arizona
J. malacophylla Standley	US*	Gentry 1449	Mexico

APPENDIX. Continued.

Species and authority	Herbarium	Collector and number	Country
J. martiusii (Pohl) Baillon	FLAS, DAV	Dehgan & Webster BD86.346	Brazil
J. mcvaughii Dehgan & Webster	DAV	Dehgan B74.206	Mexico
J. mollissima (Pohl) Baillon	FLAS	Dehgan & Webster BD86.318	Brazil
J. moranii Dehgan & Webster	DAV*	Howell 10606	Mexico
J. multifida L.	MO, KEW	Valeur 684	Dominican Republic
J. mutabilis (Pohl) Baillon	FLAS	Dehgan & Webster 312	Brazil
J. neopauciflora Pax	TEX, NY, GH, DAV	Webster et al. 17319	Mexico
J. nudicaulis Benth.	MO	Dodson & Dodson 12941	Colombia
J. olivacea Muell. Arg.	US	Pringle 6348	Mexico
J. ortegae Standley	MIN*	Ortega 6455	Mexico
J. pachypoda Pax	M*	Fiebrig 3042	Bolivia
J. pauciflora Griseb.	NY	Ekman 16169	Cuba
J. peiranoi Lourt. & O'Donn.	MO	O'Donell & Meyer 5308	Argentina
J. platyphylla Muell. Arg.	DAV	Webster & Lynch 17032	Mexico
J. podagrica Hook.	MICH	Breedlove 11810	Mexico
J. pohliana Muell. Arg.	M	Luetzelburg 26802	Brazil
J. pseudocurcas Muell. Arg.	DAV	Webster et al. 11746	Mexico
J. purpurea Rose	BM*	Palmer 785	Mexico
J. ribifolia (Pohl) Baillon	KEW*	Gardner 2303	Brazil
J. ricinifolia Pax	UC	Venturi 2350	Argentina
J. riojae Miranda	F**	Miranda 2111	Mexico
J. rufescens Brandegee	UC*	Purpus 4049	Mexico
J. rzedowskii J. Jiménez Ramírez	FLAS**	Jiménez s.n.	Mexico
J. standleyi Steyermark	MICH	Matuda 2260	Mexico
J. stevensii G. L. Webster	MO	Stevens 22902	Nicaragua
J. sympetala Blake & Standley	BM, ENCB, GH, MICH, TEX, UC, NY	McVaugh 15637	Mexico
J. thyrsantha Pax & Hoffm.	MICH	Troll 455	Bolivia
J. tlalcozotitlanensis J. Jiménez Ramírez	FLAS	Lozano 38	Mexico
J. tupifolia Griseb.	DAV, GH	Webster et al. 198	Cuba
J. vernicosa Brandegee	UC**, GH	Brandegee s.n.	Mexico
J. weddelliana Baillon	CEN	Allem 669	Brazil
J. yucatanensis Briq.	CAS	Thorn & Lathrop 40462	Mexico

* Type.
** Isotype.

A PRELIMINARY CLASSIFICATION OF *EUPHORBIA* SUBGENUS *EUPHORBIA*

Susan Carter[1]

Abstract

During preparation of the Euphorbieae for the *Flora of Tropical East Africa*, most of the 250 plus species in *Euphorbia* subg. *Euphorbia* were examined, resulting in a new approach to their classification. Comments are offered on the principal systems to date, all of which have been based on vegetative characters. In the newly proposed system, certain character changes linked with increasing succulence and a reduction in size are used to indicate development from trees, to shrubs, and then herbs, as an advancement in adaptation toward survival in arid conditions. Features of the inflorescence, capsules, and seeds are considered to be the most important in deciding relationships between groups, while vegetative features are used as indicators of development within the groups. A system of two sections based on seed characters is proposed, and the relationships between eight proposed subsections are discussed.

In preparing an account of *Euphorbia* subg. *Euphorbia* for the *Flora of Tropical East Africa* (Carter, 1988), a linear sequence in as natural a progression as possible had to be devised to accommodate the recognized species. Within the subgenus at least 250 species are known, the majority of which are native to Africa (excluding Madagascar), the rest extending westward to the Canary Islands and eastward to the Arabian Peninsula, India, and Malaysia. Examination of the approximately 90 species known in East Africa, and many more outside the geographical area of the *Flora*, has led to the outline of the system that classifies species more satisfactorily and more naturally than hitherto.

Subgenus *Euphorbia* in its strictest sense (formerly section *Diacanthium* of Boissier, which includes the type species of the genus, *E. antiquorum* L.), encompasses one of the most well-defined groups within the genus *Euphorbia*. Its species possess succulent stems and branches, with the base of each leaf surrounded by a horny pad (the *spine-shield*) bearing a pair of spiny outgrowths (*spines*), and stipules modified as *prickles*. The paired spines may become fused to produce a single spine; and the prickles may occasionally be as large as the spines, but are usually much smaller and sometimes apparently obsolete. The extent to which the prickles are obvious has affected almost all classifications. Above the spine-shield, morphologically in the leaf-axil, is the *flowering-eye*, from which the inflorescence develops, consisting of a solitary dichasial cyme, or of a group of cymes. Some Madagascan species develop apparently similar horny structures bearing one or more "spines," but these are actually modified stipules, each with an expanded horny base that flanks the leaf-scar but does not surround it. In related species these stipular structures are often developed into bristly fringes. All these species belong to the subgenus *Lacanthis* (Raf.) M. G. Gilbert (Gilbert, 1987) and are confined to Madagascar, with the exception of a few species from eastern tropical Africa.

Systems for classification to date have been artificial in their subdivisions, some extremely so, separation relying solely on vegetative characters, using habit, number of stem-angles, and number of spines and prickles borne on the spine-shield.

The first classification, by Boissier in 1862, involved less than 30 species that are recognized as such today, but included also several that are unrelated, such as the Madagascan *Euphorbia splendens* Hook. (*E. milii* Des Moul. var. *splendens* (Hook.) Ursch & Leandri), now included in subgenus *Lacanthis* (Raf.) M. G. Gilbert. Boissier defined two groups within his section *Diacanthium*: *Biaculeatae* for those species with each spine-shield bearing two spines that he considered to be stipular; and *Triaculeatae*, with three "spines" that were, in fact, two large prickles and a single (fused) spine. He further divided *Biaculeatae* into species with cylindrical as opposed to angled branches, and the latter into those with compressed (two-angled) branches versus those with three or

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more angled branches. Most species fell within this last group. He thought that *Euphorbia venenifica* Kotschy, a single-spined shrub with spirally arranged tubercles, should probably be excluded from the genus; and he mistook *E. ingens* Boiss., a large tree species, for one without spines.

1862. Classification by Boissier of Groups in Section *Diacanthium*

Diacanthium
  Biaculeatae 2 spines
    Branches cylindrical
    Branches sharply angled or ridged
      Branches compressed
      Branches 3- or many-angled
  Triaculeatae 1 (fused) spine, 2 prickles

Since Boissier's (1862) treatment, attempts to classify an increasing number of species have resulted in the vast majority falling within a group identified by two spines on each spine-shield, and three to many branch-angles, including trees, shrubs, and dwarf herbs, often with little further delimitation.

In 1904, Pax published a classification for over 80 species in section *Diacanthium*, based primarily on the number of spines and prickles present on each spine-shield. Species were assigned to groups that he named *Monacanthae*, *Diacanthae*, *Triacanthae*, *Tetracanthae*, and *Intermediae*, this last group defined by additional "upper stipular" spines on each side of the flowering-eye. By far the largest group, in which he included the unrelated species *E. splendens*, was the *Diacanthae*.

1904. Classification by Pax of Groups in Section *Diacanthium*

Monacanthae 1 (fused) spine
Diacanthae (Biaculeatae Boiss.) 2 spines
  Herbs with tuberous roots
  Shrubs or trees; branches not winged
    Leaves present
    Leaves absent; branches 3–many-angled
  Shrubs or trees; branches winged
    Leaves present
    Leaves absent; branches 2–8-winged

Triacanthae (Triaculeatae Boiss.) 1 (fused) spine, 2 prickles
Tetracanthae 2 spines, 2 prickles
Intermediae 2 spines, rudimentary prickles, upper stipular spines sometimes present

A third system, using number of branch-angles with no mention of spines, was erected in 1907 by Berger to accommodate about 50 species in cultivation at La Mortola, a large garden on the Italian Riviera owned by Sir Thomas Hanbury, where Berger was curator. His groups, without formal ranking, bore only a vague resemblance to those proposed by Pax. They included *Splendentes* (the unrelated Madagascan species with terete leafy branches allied to *E. splendens*), *Grandifoliae* (terete branches and large leaves), *Scolopendriae* (short thick stem), *Compressae* (2–3-winged branches), *Trigonae* (3–4-winged branches), and *Polygonae* (4–13-winged branches). The greatest number of species were in this last group. Single-spined species were not included, as none were in cultivation at La Mortola.

1907. Classification by Berger of Groups in section *Diacanthium*

Splendentes Branches terete; leaves present, small
Grandifoliae Branches terete; leaves present, large
Scolopendriae Herbs with short thick stem; branches ribbed; leaves absent
Compressae Trees; branches 2(–3)-winged; leaves absent
Trigonae Trees or shrubs; branches 3(–4)-winged or ribbed; leaves absent
Polygonae Trees, shrubs, or herbs; branches 4–13-ribbed; leaves absent

In 1911 and 1912, N. E. Brown's treatment of *Euphorbia* for the *Flora of Tropical Africa* was published, in which he favored no formal sections within the genus. The arrangement in his account for almost 80 spiny species presented those with single spines first, followed by those with paired spines. The latter were further loosely arranged by habit: dwarf perennial herbs, shrubs, and finally trees. In 1915 he followed a similar pattern for 21 species from the regions covered by *Flora Capensis*.

1911–1912 and 1915. Treatment by N. E. Brown of Spiny Species in *Flora of Tropical Africa* and *Flora Capensis*

Flora of Tropical Africa
  Spines single
    Shrubs or trees; leaves large, persistent
    Herbs or shrubs; leaves very small, deciduous
  Spines paired
    Plants < 1 foot high; flowering branches < 1 inch thick
    Plants > 1 foot high
      Shrubs; flowering branches < 1 inch thick
      Trees; flowering branches > 1 inch thick

Flora Capensis
  Herbs, <1 foot high
  Shrubs, 2–8 feet high
  Trees, 10–30 feet high

Pax presented a more formal classification in 1921 for the 109 African species known at that time, giving subsectional status to his groups. Following his previous (1904) system for section *Diacanthium*, he first listed species in his largest subsection, *Diacanthae*, under countries of origin

(including *E. splendens* from Madagascar), with those of East and South Africa arranged according to branch thickness. He again used the names *Triacanthae* and *Tetracanthae*, partially absorbing *Monacanthae* into *Triacanthae*. *Tetracanthae* contained species arranged according to continuation or separation of the spine-shields and height of the plants. He removed herbs with tuberous roots from his former grouping in *Diacanthae* and adopted Berger's *Scolopendriae* as a subsection to house them. The remaining species in his former *Monacanthae*, *E. venenifica*, and the early species in Brown's system related to it, all with thick cylindrical branches, he placed in a completely unrelated section of the genus—*Treisia* Haw. (1812) (*Euphorbium* Boiss. (1862))—containing plants with spirally arranged tubercles, related to the South African species *E. clava* Jacq.

1921. Formal Classification by Pax of Section *Diacanthium* into Subsections

Diacanthae 2 spines
  Flowering branches > 5 cm thick
    Spine-shields contiguous
    Spine-shields separate
  Flowering branches 2–3 cm thick
Triacanthae 1 (fused) spine, 2 prickles
Tetracanthae 2 spines, 2 prickles
  Spine-shields contiguous
    Herbs to 20 cm high
    Shrubs 1.5 m high or more
    Trees
  Spine-shields separate
    Herbs to 30 cm high
    Shrubs 1 m high or more
    Trees
Scolopendriae Stems short, thick
Section *Treisia* Leaves present, spirally arranged on thick, erect stems

In 1931, Pax & Hoffmann reduced *Diacanthium* to subsectional status under section *Euphorbium* Boiss. (1862), including in the latter all succulent stemmed species of the genus. They adopted Berger's system more fully in order to regroup the now unwieldy numbers of disparate species in Pax's original (1921) concept of *Monacanthae*, *Diacanthae*, and *Intermediae*, using instead all Berger's group names and citing Berger's species as examples. They added to these Pax's own *Triacanthae* and *Tetracanthae*, once more as groups without formal rank.

1931. Classification by Pax and Hoffmann of Section *Euphorbium* subsection *Diacanthium* into Groups

Splendentes Madagascan species
Grandifoliae Spine-shields separate; leaves large
Scolopendriae Herbs with a short thick stem
Compressae Trees; branches 2-winged
Trigonae Trees or shrubs; branches 3(4)-winged
Polygonae Trees or shrubs
  Branches 3–4-angled
  Branches 4–5(–6)-angled
  Branches 5–8-angled
  Branches 9–13-angled
Triacanthae Shrubs; 1 (fused) spine, 2 prickles
Tetracanthae Shrubs or herbs; 2 spines, 2 prickles

In 1941, White, Dyer & Sloane broke with tradition in devising a more natural sequence for 41 species of spiny *Euphorbia* from South Africa in groups without formal names. These were defined on the basis of habit (dwarf herbs, shrubs, and trees), but position of the capsule and arrangement of the cyathia were also used as important features in deciding relationships.

1941. Treatment by White, Dyer & Sloane of South African Spiny Species

Dwarf herbs, 1 foot high or less
  Capsules exserted
  Capsules sessile
Shrubs, 1–10 feet high
  Branches < 1 inch thick; cyathia horizontally arranged
  Branches > 1 inch thick; cyathia vertically arranged
    Cymes solitary in each flowering-eye
    Cymes 1–4 in each flowering-eye
      Capsules small, exserted
      Capsules large, subsessile
Trees
  Cymes 1–5 in each flowering-eye; cyathia vertically arranged
  Cymes solitary in each flowering-eye; cyathia horizontally arranged

The two latest treatments reverted to the number of branch-angles and spines as criteria for groupings. Jacobsen (1954, 1960) divided all succulent species of *Euphorbia* (but without formal ranking) into *Pedunculicantha* with spines derived from the hardened peduncles of the inflorescence, and *Stipulicantha* with "thorns" derived, he considered, from stipules. This latter group, which concerns us here, he further separated (Jacobsen, 1960) into sections *Euphorbia* (*Diacanthium* of earlier authors and Jacobsen, 1954), *Monacanthium*, and *Triacanthium*. *Euphorbia* was by far the largest of his sections, divided further into two groups (no rank designated), the *Teretes* and *Costatae*, the arrangement within them based on Berger's (1907) treatment. The *Teretes* consisted of the former *Splendentes* and *Grandifoliae*. Within the *Costatae* he enlarged Berger's (1907) and Pax's (1921) concept of the *Scolopendriae* considerably, to include all species with a thick, fleshy, or tuberous root giving rise to tufted branches. The *Trigonae* and *Polygonae* he amalgamated to include all other species—trees, shrubs, and herbs—apart from those in the *Compressae*. Sections *Monacanthium* and *Triacanthium*, with equal status

to *Euphorbia*, he used to accommodate the few remaining single-spined species.

1954 AND 1960. INFORMAL CLASSIFICATION BY JACOBSEN OF SECTIONS AND GROUPS IN *STIPULICANTHA* USING BERGER'S (1907) AND PAX & HOFFMANN'S (1931) ARRANGEMENTS

Euphorbia (Diacanthium) 2 spines
  Teretes
    Group 20 (Splendentes)
    Group 21 (Grandifoliae)
  Costatae
    Group 22 (Scolopendriae)
    Group 23 (Compressae)
    Group 24 (Trigonae and Polygonae)
Monacanthium 1 (fused) spine
Triacanthium 1 (fused) spine, 2 prickles

Rauh (1967) loosely followed this treatment, using sections only: *Monacanthium, Triacanthium*, and also *Diacanthium* (instead of *Euphorbia*), which included, once again, the greatest number of species. However, he removed Jacobsen's additions to the *Scolopendriae* to section *Tetracanthium*, adopting for the latter Pax's original (1904) concept of *Tetracanthae* as those species with 4 spines (actually 2 spines and 2 prickles) on each spine-shield.

1967. CLASSIFICATION BY RAUH OF SPINY SPECIES INTO SECTIONS

Diacanthium (Euphorbia) 2 spines; trees, shrubs, and dwarf herbs
Monacanthium 1 (fused) spine; shrubs
Triacanthium 1 (fused) spine, 2 prickles; herbs
Tetracanthium 2 spines, 2 prickles; herbs

All these arrangements have been based primarily on vegetative characters, with features of the inflorescence often ignored as sectional indicators. As an example, N. E. Brown (1911–1912) relied almost entirely on number of branch-angles and detail of the spinescence for dichotomy in his long key. White, Dyer & Sloane's (1941) arrangement was the only one to diverge from this system, using floral as much as vegetative characters to group the South African species. Dyer suggested that in separating the spiny species into related groups, importance should be given to the cyme and cyathial arrangement in each flowering-eye, and the shape of the capsule should also be considered.

Succulence has developed as a device for survival in arid regions. Within the genus *Euphorbia*, adaptation to increasingly arid habitat conditions has involved an increase in succulence of the stem and branches, and a decrease in the size of the plant-body. Representatives of stages in this progression can be found in subgenus *Euphorbia*, ranging in habit from trees, to shrubs, and finally dwarf herbs. The weakest development of succulence—the least advanced state in this adaptation—is found in forest trees with thinly fleshy, winged branches. An increase in succulence of the stem and branches, associated with a decrease in size of the plant-body, is evident in related trees of drier habitats, and in shrubs and herbs of more arid regions, where adaptation to extreme conditions has resulted in the most advanced state: reduction to a small globose body. Other character changes associated with this increased adaptation occur in a reduction in leaf-size, development of the spinescence, the structure of the cyme, a reduction of the perianth-lobes in the female flower, capsule shape and size, and features of the seed.

Comparing features of the least-succulent trees with those of the most-succulent herbs, it is possible to determine which characters have undergone the greatest change during adaptation to an arid environment, and thus which state can be regarded as primitive and which advanced. Apart from a reduction in size linked with habit, from trees to globose-bodied herbs, the large persistent leaves of some trees and shrubs, as would be expected, have given way in most species to very small or minute leaves that are quickly deciduous. The almost rounded, obtusely triangular spine-shields of many trees have become decurrent, which in turn has led to terete branches with spirally arranged tubercles, becoming angled with longitudinal ridges crowned by spine-shields that are sometimes joined to form a continuous horny margin. Stipules, although small, are soft and sometimes almost leaflike in many tree species, whereas in the shrubs, and especially the herbs, they have hardened and been modified into prickles. In most trees and many of the shrubs, several cymes, sometimes branched, are grouped in each flowering-eye, coupled with a vertical arrangement of the lateral cyathia. Most herbs and some shrubs develop one cyme at each flowering-eye, considerably smaller and with lateral cyathia horizontally arranged. Among the trees a 3-lobed perianth is sometimes obvious at the base of the ovary and capsule, which is also relatively large and acutely 3-angled. Usually the perianth is no more than a rim in herbs, shrubs, and many trees, with the capsule reduced in size and obtusely 3-lobed. Finally, although there seems to be no special advantage in such a development, subglobose smooth seeds are characteristic of the trees, but those of most herbs and some shrubs are ovoid and tuberculate.

Using these features and the way in which they have apparently developed within groups of obvi-

TABLE 1. Character states, distribution, and representative species in proposed subsections of sections *Euphorbia* and *Tetracanthae* of subgenus *Euphorbia*.

Subsection	Habit	Leaves	Branches	Spinescence	Cyme arrangement
Section *Euphorbia*					
Euphorbia	Trees	Large, persistent	Terete to winged	Shields triangular, separate	Several in each flowering-eye
Ingentes	Trees and shrubs	Large, persistent or small and deciduous	Winged to angled	Shields triangular, separate, disintegrating	1–many in each flowering-eye
Spirales	Trees and shrubs	Large, persistent	Angled to terete	Shields triangular, separate; spines paired or single	Solitary
Scolopendriae	Small herbs; roots fleshy	Obvious, persistent or small and deciduous	Terete or 2–5-angled	Shields triangular, separate	Solitary
Segmentes	Trees, shrubs, and herbs; roots tuberous	Small, deciduous	Winged, segmented, 2–8-angled	Shields joined or slightly separated	1–many in each flowering-eye
Costatae	Trees and large shrubs	Small, deciduous	Shallowly segmented, 3–7-angled	Shields separated or joined	1–3–many in each flowering-eye
Section *Tetracanthae*					
Sessiles	Shrubs and herbs; roots fleshy or tuberous	Small, deciduous	4-angled, rarely more	Shields separated, rarely joined; spines paired or single	Solitary
Pedicellares	Shrubs and herbs; roots fleshy or fibrous	Small, deciduous	4-angled to 16-ribbed	Shields separated or joined	Solitary

TABLE 1. Continued.

Subsection	Cyathial arrangement	Capsule	Female perianth	Geographical range	Examples
Section *Euphorbia*					
Euphorbia	Vertical	Large, acutely 3-lobed, exserted	Obvious	Thailand west to India, Arabian Peninsula, and northern tropical Africa	*E. lactea, E. nerifolia, E. antiquorum, E. qarad, E. teke*
Ingentes	Vertical or horizontal	Globose, fleshy, just exserted	Obvious	Arabian Peninsula, West Africa, eastern tropical Africa from Sudan south to Natal	*I. ammak, I. kamerunica, I. abyssinica, I. ampliphylla, I. ingens*
Spirales	Horizontal	Large, acutely 3-lobed, exserted	Reduced to a rim	West and central tropical Africa	*S. desmondii, S. sudanica, S. poissonii, S. venenifica*
Scolopendriae	Horizontal	Acutely 3-lobed, exserted on a recurved pedicel	Reduced to a rim	Angola to Mozambique and south to the Cape	*S. imitata, S. decidua, S. knuthii, S. stellata*
Segmentes	Vertical	Large, acutely 3-lobed, subsessile	Obvious or reduced to a rim	Arabia and Somalia south to Mozambique and west to Angola, Namibia, and the Cape	*S. cactus, S. ballyi, S. nyikae, S. breviarticulata, S. cooperi, S. grandicornis, S. enormis*
Costatae	Vertical or seldom horizontal	Large to small, angled to lobed, exserted	Reduced to a rim	Somalia south to Mozambique, Angola, Namibia, and the Cape	*C. robecchii, C. wakefieldii, C. confinalis, C. parviceps, C. grandidens, C. griseola*
Section *Tetracanthae*					
Sessiles	Horizontal	Small, obtusely lobed, subsessile	Reduced to a rim	Arabia and Somalia south to Mozambique, Angola, Namibia, and the Cape	*S. triaculeata, S. polyacantha, S. uhligiana, S. angustiflora, S. malevola, S. schinzii*
Pedicellares	Horizontal	Small, obtusely lobed, exserted on a recurved pedicel	Reduced to a rim	Arabia, Socotra, northeast and eastern tropical Africa	*P. fruticosa, P. spiralis, P. phillipsiae, P. turbiniformis, P. heterochroma*

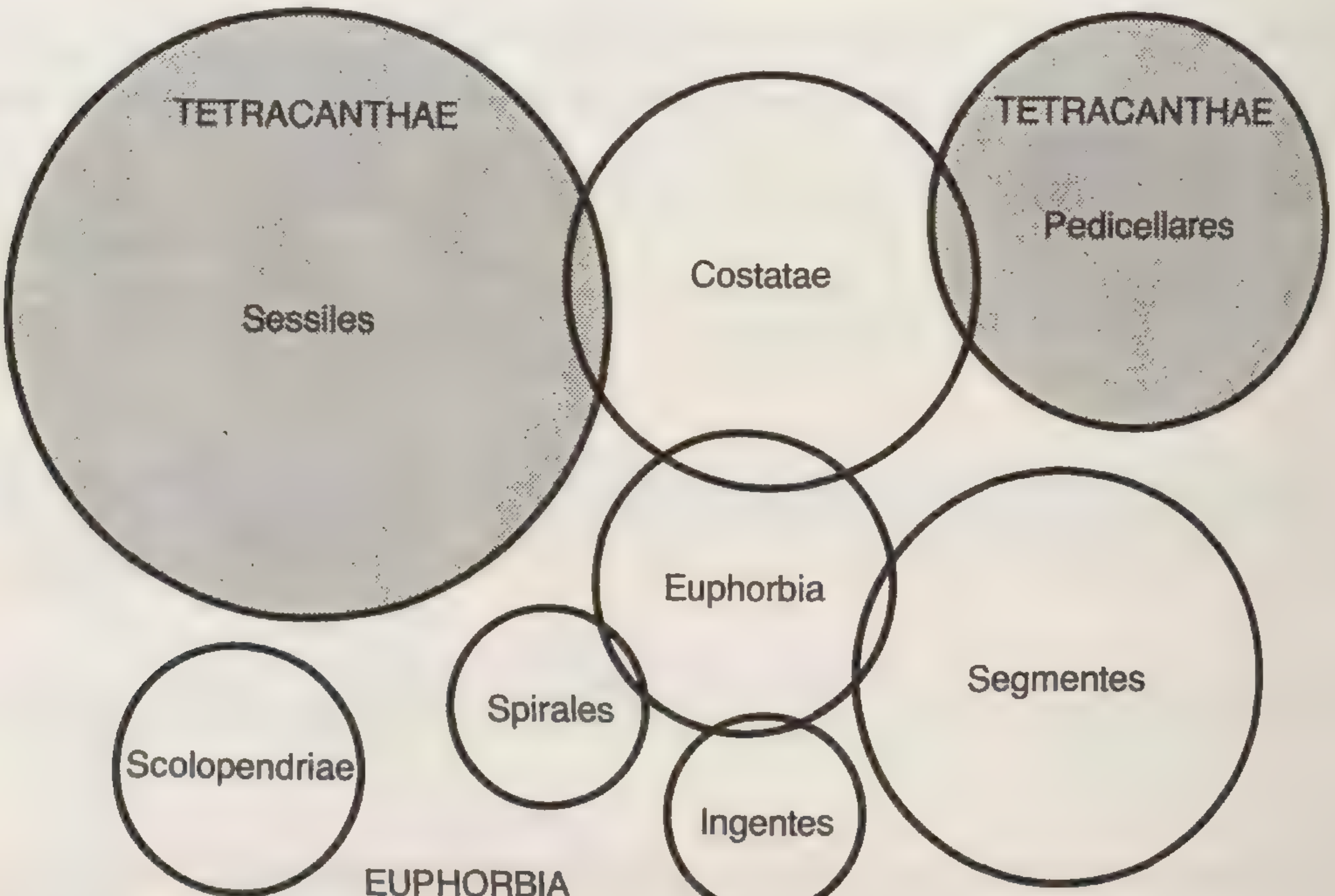

FIGURE 1. Diagramatic representation of relationships between groups (subsections) within subgenus *Euphorbia*, with two sections: *Euphorbia* and *Tetracanthae*. Circle-size is proportional to the number of species in each subsection.

ously closely related species, an outline scheme for the classification of the 250 plus species in subgenus *Euphorbia* is presented here, with two sections and several possible groups or subsections. Inevitably, there is some sharing of character states between groupings, and this has been used to indicate trends in development. The most obscure relationships occur between the smaller groups containing species exhibiting an early, more primitive stage in development, whereas those with features at the most advanced stage are the most easily defined. These are also represented by a much larger number of species, among which obvious subgroups or series have emerged, with some apparently still developing. However, characteristics of the seed are consistent within groups, and this feature is used to separate the subgenus initially into two sections: section *Euphorbia*, containing species with more primitive character states, and all with smooth, globose or subglobose seeds; and section *Tetracanthae*, containing species with more advanced characteristics, all with tuberculate, more-or-less ovoid seeds (see Fig. 1 and Table 1).

Among the few representative species (about 12–15) of the subgenus in India, Malaysia, and the Far East, all possess features at a stage regarded here as primitive, with only slight modifications in some species toward an adaptation for survival in a drier environment. As an example, *Euphorbia neriifolia* L. is a tree, with terete branches, rounded spine-shields spirally arranged, large leaves (to 30 cm long), triangular flexible stipules, several long-pedunculate branching cymes from each flowering-eye, a lobed perianth below the ovary, an exserted deeply lobed capsule, and smooth globose seeds. *Euphorbia antiquorum* L. is modified only slightly in its obscurely 3-angled branches, smaller, less persistent leaves, and fewer-branched cymes. Other species show a greater tendency toward both angled branches and reduction in leaf size. To the west, in the Arabian Peninsula, *E. qarad* Deflers shows a reduction in size to a large shrub and to very small deciduous leaves. In the African continent, primitive states are most evident in a group of probably four closely related species from the forest region of western Uganda westward across northern Zaire to Cameroon. These include *E. teke* Pax, modified only in its obscurely 4-angled branches.

This group of species, with characters at the most primitive stage of development, corresponds most nearly with Berger's (1907) group *Grandifoliae* and Jacobsen's (1960) *Teretes*, excluding the *Splendentes*. Since it contains the type species of the genus it must, under present rules, be referred to as *Euphorbia* at whatever rank.

Several groups (or possible subsections) appear to have developed from this basic group ("subsec-

tion *Euphorbia*"), with different features undergoing change. One that I propose calling the "*Ingentes*" accommodates about 10 species with a wide distribution covering most of the African continent and beyond to the Arabian Peninsula. Modifications shared by all its species are angled or sometimes winged branches, with more closely set spine-shields disintegrating at maturity to become corky and powdery, simple cymes and only slightly exserted, usually fleshy subglobose capsules, which nevertheless harden and become acutely 3-lobed at dehiscence. *Euphorbia ampliphylla* Pax (*E. obovalifolia* auct. non A. Rich.), the species most closely related to those of "subsection *Euphorbia*" has 3–4 deeply winged, thinly fleshy branches, and large leaves (to 15 cm long) persistent on young growth. It is the largest of all *Euphorbia* species, reaching 30 m in height, surviving only in mist forests above 1800 m, from Eritrea southwards to northern Zambia and Malawi. At lower altitudes most species show an increase in succulence of the branches and decrease in leaf size. *Euphorbia ingens* Boiss., from southern Africa, has more fleshy, angled rather than winged branches, and leaves smaller (to 7 cm long) on seedlings and young growth, but tiny and deciduous on mature growth. *Euphorbia abyssinica* J. F. Gmel., from drier regions of northeast Africa, is very similar, but has stouter, 5–8-angled branches. The closely related *E. ammak* Schweinf. occurs in the Arabian Peninsula, and *E. kamerunica* Pax, a 4-winged species, in West Africa. *Euphorbia canariensis* L., from the Canary Islands, appears to share most features of this group but also shows the most extreme modifications. It is a large shrub instead of a tree, with single simple cymes, horizontally instead of vertically arranged cyathia, and capsules that are only slightly fleshy. Members of this group have previously been placed with other unrelated species depending on the number of branch angles.

A group here called the "*Spirales*" accommodates about nine very distinct, closely related species with a limited distribution in West and Central Africa. Modifications found in such species as *Euphorbia desmondii* Keay & Milne-Redh. and *E. sudanica* Chev. are evident as a reduction in size to shrubby trees, angled branches, solitary cymes with cyathia arranged horizontally, and the perianth of the female flower reduced to a rim. Specialization has led to a subgroup of smaller shrubs that have spine-shields so densely placed in numerous spiral series that thick cylindrical branches have resulted. Furthermore, the paired spines appear fused together early in the seedling stage, after which only single spines are produced. These later deteriorate so that the mature plants sometimes appear to be entirely without spines. *Euphorbia venenifica* Kotschy and *E. poissonii* Pax are typical of this subgroup, one that Pax and other authors had such difficulty in placing.

Reduction to tuberous-rooted herbs has taken place in one group, which has been apparent as distinct since Boissier's (1862) classification, and which even now is difficult to relate to other groups. This was given the name *Scolopendriae* by Berger and formalized as a subsection by Pax (1921). Its species, all from southern tropical Africa, are small herbs or geophytes, characterized by a large tuberous root, extremely short stem branching at or below ground level, small rounded spine-shields, and acutely lobed capsules exserted on a recurved pedicel.

Two series appear to have developed within the group. In one, a progression can be shown from thin branches with very small spine-shields and spines, as in *Euphorbia knuthii* Pax, to leafless angled or winged branches with strong spines, as in *E. stellata* Willd.

The second series, in a group of closely related species, shows a progression from such species as *Euphorbia imitata* N. E. Br., with persistent leaves, to *E. decidua* P. R. O. Bally & L. C. Leach, with a development of the tuberous root to a spherical body from which deciduous branches develop separately from the cymose inflorescences, bearing tiny deciduous leaves and small rounded spine-shields.

The most probable relatives of the group seem to be species in "*Spirales,*" through a common ancestor and an early reduction of the shrubby form. Similarities between the two groups lie in the rounded spine-shields, persistent leaves, cyme and cyathial structure and position, and especially the sharply angled exserted capsules with smooth globose seeds.

Another easily defined group within section *Euphorbia* is one I propose calling the "*Segmentes,*" incorporating Pax's *Intermediae*. Some primitive features are retained, namely several cymes at each flowering-eye together with vertically arranged cyathia, often an obvious lobed perianth, large acutely 3-lobed capsules, and smooth globose seeds. There are some tree species, but most are shrubs; branches are distinctly winged and constricted at intervals into rounded or oblong segments; the spine-shields have become so decurrent that in almost all species they have joined to form a horny margin along the branch-angles, often very stout and occasionally giving rise to further spines flanking the flowering-eye (Pax's *Intermediae*); leaves are tiny and deciduous, with stipules hardened into very short or usually rudimentary prick-

les. One of the least advanced species is *Euphorbia nyikae* Pax from East Africa, bearing some similarity to *E. lactea* Haw. from Sri Lanka in "subsection *Euphorbia*," but with decurrent spine-shields.

The 40 or more species within the "*Segmentes*" show a reasonably successful adaptation to an increasingly arid environment. The tendency is toward a reduction in size to shrubs, and eventually fleshy herbs, together with an increase in the size of the rootstock to large and tuberous. At the same time, the capsule becomes subsessile among most of the shrubs, and totally sessile in the herbs. Several series of species show this progression. In East Africa, for example, there are a tree species *Euphorbia bussei* Pax, a shrub *E. breviarticulata* Pax, and a tuberous-rooted herb *E. buruana* Pax. Further south a similar progression is shown by the tree *E. cooperi* A. Berger, the shrub *E. grandicornis* N. E. Br., and the herb *E. enormis* N. E. Br.; while in the more extreme habitat conditions of Angola and Namibia shrubs such as *E. coerulescens* Haw. and tuberous-rooted herbs related to *E. opuntioides* Hiern may be found. The complex is distributed as far north as the Arabian Peninsula, with the shrub *E. cactus* Schweinf., and in northern Somalia the shrub *E. ballyi* S. Carter together with an unnamed dwarf tuberous-rooted species.

A most diverse group of species, with variable characteristics and also a wide distribution, has close relationships with "subsection *Euphorbia*," but differs consistently in a number of distinct modifications. Among primitive features, most species are trees and most have several cymes at each flowering-eye, with vertically arranged cyathia. However, some species have a tendency to develop a shrubby habit, and cymes become solitary, with the cyathia arranged horizontally. Branches are always angled (3–7), giving the group its name of "*Costatae*" (Jacobsen's (1960) name without formal rank), and occasionally winged, with spine-shields decurrent and either separate or forming a continuous horny margin. Leaves are tiny and quickly deciduous, but stipules are sometimes obvious and flexible—a primitive feature—or more usually are present as rudimentary prickles or are only vestigial. The perianth is reduced to a rim. Pedicel length of the capsule is variable, as is capsule size, with the larger capsules usually acutely angled on stout, often curved pedicels, and the smaller ones more obtusely lobed on slender recurved pedicels.

A number of tree species from Angola related to *Euphorbia edouardii* L. C. Leach and *E. parviceps* L. C. Leach have retained most of the more primitive features, which they share with such species as *E. robecchii* Pax from East Africa, and *E. evansii* Pax and *E. confinalis* R. A. Dyer from further south. *Euphorbia robecchii* in turn seems to bear some relationship to *E. qarad* in "subsection *Euphorbia*," through an unnamed intermediate shrubby tree that occurs in Djibouti.

In East Africa a series of several tree species with limited distributions has developed, including the narrowly 3-winged *Euphorbia wakefieldii* N. E. Br. with small triangular spine-shields and *E. quinquecostata* Volkens with 5-angled branches and decurrent spine-shields that become joined as growth matures. Both species have small, obtusely lobed capsules that are well exserted. This series culminates in *E. classenii* P. R. O. Bally & S. Carter, a 1-m-high shrub with 6–8-angled branches, decurrent spine-shields, solitary cymes with horizontally arranged cyathia, exserted capsules, and smooth, more or less ovoid seeds.

A comparable series has arisen in southern Africa, including the tree species *Euphorbia grandidens* Haw., with 3-angled branches, small triangular spine-shields, and slightly exserted capsules, and *E. zoutpansbergensis* R. A. Dyer, with 6-angled branches, decurrent spine-shields becoming joined, and obtusely lobed, exserted capsules. Shrubby species such as *E. avasmontana* Dinter, with a stout horny margin to usually 5-angled branches, have developed especially in the semi-desert regions of southwest Africa.

Most of these species have a tendency to produce more than one cyme at each flowering-eye, with vertically arranged cyathia. However, *Euphorbia griseola* Pax, from south tropical Africa, is one species that has developed as a small tree with a short trunk (subsp. *zambiensis* L. C. Leach) and also as a low-growing spreading shrub (subsp. *griseola*), but always with decurrent spine-shields sometimes joined, solitary cymes with horizontally arranged cyathia, and small, well-exserted, deeply lobed capsules containing smooth globose seeds. A further development has produced a series of a few species related to *E. perangusta* R. A. Dyer, with the fleshy root developed into a large tuber, and decurrent spine-shields on short winged branches that have become almost segmented. These bear a superficial resemblance to the reduced herbs of the "*Segmentes*," the overriding difference being that capsules are small and well exserted instead of large and sessile.

Several of the 40 or so species in this widely distributed group "*Costatae*" can be considered as linking species with those in the two groups that have been the most successful in terms of species

numbers and adaptation to arid conditions. These show the most advanced and none of the primitive character states postulated for "subsection *Euphorbia*." Also, one outstanding feature that all the species possess is an ovoid tuberculate rather than globose and smooth seed. On this basis I have separated them into section *Tetracanthae*, which Pax (1921) formalized and which included very few species regarded here as belonging instead to section *Euphorbia*. Pax's (1921) definition of the section allowed for the inclusion of all species bearing four spines on the spine-shields. However, this is exceedingly misleading. All species within the larger category of subgenus *Euphorbia* bear two spines, outgrowths from the horny pad surrounding the base of the leaf, together with a pair of stipules that are evident in every species. These stipules can be triangular, flexible, and almost leaflike in some tree species with more primitive characteristics; or they can be modified into obvious prickles or occasionally short spines in species at a more advanced stage of development. They can equally be rudimentary or visible only with a powerful hand lens among species of most groups (or subsections) in section *Euphorbia* and in both groups of section *Tetracanthae*. However, within this latter section, modification into a pair of obvious prickles is a hallmark, although by no means universal, of the larger group—called here "subsection *Sessiles*"—the definitive feature being a small, obtusely lobed sessile or usually subsessile capsule, at the most only just exserted from the involucre. Species in the smaller, totally distinct group—"subsection *Pedicellares*"—also possess a small obtusely lobed capsule, but this is always well exserted on a slender recurved pedicel. Stipules are evident as short prickles, or more often are rudimentary or vestigial. In both subsections, herbs with an often large fleshy root predominate, with relatively few shrubs, which are rarely more than 1 m high. Other advanced features lie in tiny deciduous leaves, decurrent spine-shields, solitary cymes with horizontally arranged cyathia, and the perianth reduced to a rim.

The "*Sessiles*" includes more than 80 species, distributed mostly in eastern and southern tropical Africa, but extending also to southwest Africa, and northeastward to the Red Sea Hills of Sudan and the Arabian Peninsula. With few exceptions branches are 4-angled, with decurrent spine-shields that are seldom joined. Some species in the "*Costatae*" can be regarded as providing a link with other, usually shrubby and possibly related species in the "*Sessiles*," but despite similarities in spinescence and inflorescence characters, the difference between ovoid tuberculate seeds and globose smooth seeds always provides a positive means for sectional identification. *Euphorbia dumeticola* P. R. O. Bally & S. Carter in the "*Costatae*" is a small tree from central Tanzania with solitary cymes, horizontal cyathia, and only shortly exserted capsules, which is perhaps related to the shrub *E. proballyana* L. C. Leach in the "*Sessiles*," endemic in the same area. Similarly, several species from southern Africa in the "*Costatae*," e.g., the shrub *E. waterbergensis* R. A. Dyer, which possesses shortly exserted, obtusely lobed capsules, suggest a possible link with shrubs such as *E. lydenbergensis* R. A. Dyer in the "*Sessiles*."

As would be expected in a large group at such an advanced stage of adaptation, a number of distinct subgroups, or series, of closely related species have evolved. For example, in southern Africa, *Euphorbia schinzii* Pax is one of a number of very similar species with spreading tufts of short erect branches and, itself, is identified in several forms, differing in stem thickness and spine color. The strange *E. corniculata* R. A. Dyer, from Mozambique, with enlarged spine-shields and apparently obsolescent prickles, appears to be related. Further north, the more shrubby *E. malevola* L. C. Leach from Zimbabwe has obvious affinities with *E. ambroseae* L. C. Leach from Mozambique and in turn *E. isacantha* Pax from southern Tanzania. One small subgroup of distinctive species with almost peltate involucral glands, related to *E. angustiflora* Pax, is confined in distribution to central and southwest Tanzania. Other subgroups have evolved in East Africa, such as *E. uhligiana* Pax and its relatives, all with a distinctive T-shaped spine-shield, and the development among species from more arid areas of a vertical series of cymes that mature in succession in each flowering-eye. Several forms have emerged with extreme modifications of the spinescence: the rhizomatous species *E. taruensis* S. Carter from Kenya has extremely slender spine-shields bearing obvious prickles, but spines that are rarely more than rudimentary; and the subscandent *E. cryptospinosa* P. R. O. Bally has usually 7-angled stems, with spine-shields joined into wide continuous ribs and minute spines on young growth only that cannot be seen except with the aid of a hand lens.

Besides *Euphorbia cryptospinosa* from Kenya and relatives in southern Somalia, species with more than four angles have also evolved in southwestern Africa, e.g., *E. kaokoensis* L. C. Leach. In the northeast, as far as the Red Sea Hills in Sudan, *E. polyacantha* Boiss. has developed into a 6–7-angled shrub with a stout spinescence. A related unnamed species with more slender 4–5-angled

branches occurs throughout the hilly regions from Djibouti eastward across northern Somalia.

A feature that has developed principally among plants of drier regions in the northeast is the fusion of the paired spines in the seedling stage, when this is no more than 2–3 cm high, to produce what appears to be a single spine. The presence or absence of prickles led former workers to mistakenly separate these species into groups with one or three "spines" (e.g., Pax's (1904) *Monacanthae* and *Triacanthae*), including the shrubs related to *E. venenifica*. One subgroup, *Euphorbia graciliramea* Pax and its relatives, has developed in the Rift Valley of northern Tanzania and southern Kenya as herbs with a large fleshy root producing tufts of short branches and small spine-shields with rudimentary prickles. Another group from northern Kenya and Ethiopia, related to *E. monacantha* Pax, has developed a short thick stem with numerous branches radiating from a central growing point and varying in length between species. Other species without this distinctive "medusoid" habit can be related to *E. triaculeata* Forssk. from the Arabian Peninsula. Several unnamed species in this subgroup occur in Somalia and eastern Ethiopia. Intermediate forms, with spines only partly fused, are found in *E. schizacantha* Pax, with a short, thick, many-angled stem and thin, trailing, 4-angled branches; and *E. glochidiata* Pax, with a 2-m-high stem and undifferentiated branches. Both species and their relatives occur in the dry deciduous bushland of northeast Kenya, southeast Ethiopia, and southern Somalia.

Within subgenus *Euphorbia*, the most successful adaptation to a hostile environment is shown by members of "subsection *Pedicellares*." The group has diversified in east and especially northeast Africa, with representatives also in the Arabian Peninsula and Sococtra, and a disjunct distribution in Morocco and the Canary Islands.

At the southern limit of distribution of this group, in northeast Tanzania, *Euphorbia heterochroma* Pax is a shrub to 2 m high with 4-angled branches, evidently related to *E. classenii* in the "*Costatae*," which differs in its 6–8-angled branches and distinctly separated spine-shields, as well as its smooth globose seeds. In drier inland areas in Kenya, Uganda, and southern Ethiopia, *E. heterochroma* gives way, in an obvious progression, to shorter more sturdy shrubs, with up to 8 angles, and spine-shields joined in a wide horny margin, culminating in the various forms of *E. tescorum* S. Carter.

In Somalia and the Ogaden region of eastern Ethiopia, adaptation to the very specialized semi-desert conditions created by a limestone soil and outcrops of pure gypsum has led to the development of many narrowly endemic species. Stems and branches have become many-angled—up to 18—and reduced in size, finally to a globose body, evident in several species. *Euphorbia columnaris* P. R. O. Bally presents one extreme, as an unbranched stem with up to 16 angles and a cluster of up to 30 cymes, maturing successively, at each flowering-eye. *Euphorbia turbiniformis* Chiov. presents another, as a small spherical body that is almost buried in the soil and has lost all its spines. *Euphorbia gymnocalycioides* M. G. Gilbert & S. Carter is an intermediate form, with up to 18 ridges of tubercles crowned by tiny, weakly horny spine-shields occasionally bearing vestigial spines. *Euphorbia piscidermis* M. G. Gilbert belongs here also, having developed a globose body and an extreme modification of the spine-shield into a fringed "scale," with a pair of minute spines evident only on tiny seedlings.

There are numerous species from Somalia (many still unnamed) in several series, leading to similar extremes, usually in the form of dwarf "cushion"-forming plants with 5 to many angles on short, densely packed branches. Some have small, distinctly separated spine-shields, like *Euphorbia ellenbeckii* Pax, while others have narrow horny margins along the angles, like *E. phillipsiae* N. E. Br.

In common with other examples in Africa of a northeast-northwest relationship, a disjunct group of species with obvious similarities occurs in the Canary Islands and Morocco. Several shrubby species related to *Euphorbia echinus* Hook.f. & Coss., from the Moroccan coast, possess many-angled branches and spine-shields joined in a narrow margin along the angles, as well as small capsules exserted on recurved pedicels.

Other species of the "*Pedicellares*" extend into the Arabian Peninsula in at least three forms of *Euphorbia fruticosa* Forssk. and occur in Socotra as *E. spiralis* Balf.f. The large shrub *E. abdelkuri* Balf.f. from Socotra, with 6–8-angled, spineless branches, also belongs here, the spines and spine-shields having been lost during the process of evolution (but which are nevertheless present at the seedling stage), possibly due to the absence of browsing animals on a small island.

Subgenus *Euphorbia* is arguably the most easily and satisfactorily defined of all the major groups within the genus, at whatever rank, and as such could be separated as a genus in its own right (which begs the question: what to do with all the other groups not as readily separated as *Chamaesyce*?). It shows as great, if not a greater, diversity

of form as the rest of the genus put together, from giant forest trees, to shrubs, herbs, and even geophytes. It is evident that vegetative characters used by previous authors can often provide some indication of the smaller group to which a species belongs, but they are not, on their own, sufficient to identify its relationships positively. In the scheme proposed here (see Fig. 1), characters of the much more stable features of seed, capsule and inflorescence are of prime importance in determining relationships. Habit and vegetative characters of spinescence and branch structure play a secondary role. At the same time they are used as indicators of development within groups, as well as between them, during the gradual adaptation to an arid environment.

Relationships of this very distinct and apparently isolated group of species are not easily determined. Gilbert (1987) has suggested, with some reservation, that it could have been derived from section *Tirucalli* Boiss. (Boissier, 1862). Species of this occur in all the drier regions of Africa, the Arabian Peninsula, and Madagascar, with small leaves quickly deciduous from succulent, cylindrical branches, leaving prominently calloused leaf-scars sometimes surrounded by glandular tissue that could perhaps be homologous with the spine-shield. In personal discussions with Gilbert, it now seems to us that a more likely relationship could lie with a small group of fleshy-stemmed shrubs related to *Euphorbia synadenium* Ridley, from evergreen forests of India and Malaysia. These possess large leaves, with small, persistent stipules, that are leaf-like and often stiffly pointed, resembling the stipular prickles on the spine-shields of tree species in "subsection *Euphorbia*." This would indicate that subgenus *Euphorbia* (the pair-spined species) may have originated in Asia and migrated to northern Africa at about the time that the continents were breaking up and Madagascar became separated. Development and proliferation within Africa followed as the continent became drier. The relatively few forest species of today retain primitive characteristics, while those of the larger, more successful groups, possessing characters at the most advanced state of adaptation for survival in an arid environment, are found in the extreme habitat conditions of semi-desert regions, notably in southwest Africa, and especially in the northeast, in the Horn of Africa.

This proposed classification of subgenus *Euphorbia* is based on evidence gained from examination of almost all the species known today. Some gaps remain, especially among the groups with features at the least advanced stage of development and fewer representative species; but these gaps are not great, and it is hoped that, as discoveries of new species are made, they will be filled, and the feasibility of the scheme outlined here will be confirmed.

Literature Cited

Berger, A. 1907. Sukkulente Euphorbien. Ulmer, Stuttgart.

Boissier, P. E. 1862. Euphorbiaceae, Euphorbieae. Pp. 1–188 *in* A. de Candolle (editor), Prodromus Systematis Naturalis Regni Vegetalis 15(2). Masson & Son, Paris.

Brown, N. E. 1911–1912. Euphorbiaceae. Pp. 448–608 *in* W. T. Thiselton-Dyer (editor), Flora of Tropical Africa, 6(1). Reeve, London.

———. 1915. Euphorbiaceae. Pp. 220–375 *in* W. T. Thiselton-Dyer (editor), Flora Capensis 5(2). Reeve, London.

Carter, S. 1988. Euphorbieae. Pp. 409–564 *in* R. M. Polhill (editor), Flora of Tropical East Africa, Euphorbiaceae. Balkema, Rotterdam/Brookfield.

Gilbert, M. G. 1987. Two new geophytic species of *Euphorbia* with comments on the subgeneric grouping of its African members. Kew Bull. 42: 231–244.

Haworth, A. H. 1812. Synopsis Plantarum Succulentarum. Taylor, London.

Jacobsen, H. 1954. Handbuch der Sukkulenten Pflanzen (Band 1). Fischer, Jena.

———. 1960. A Handbook of Succulent Plants, Vol. 1. Blandford Press, London.

Pax, F. 1904. Monographische Übersicht über die afrikanischen Arten aus der Sektion *Diacanthium* der Gattung *Euphorbia*. Engl. Bot. Jahrb. 34: 61–85.

———. 1921. Die Pflanzenwelt Afrikas, Euphorbiaceae. Pp. 1–68 *in* Engler (editor), Die Vegetation der Erde 3(2). Engelmann, Leipzig.

——— & K. Hoffmann. 1931. Euphorbiaceae. Pp. 11–233 *in* A. Engler et al. (editors), Die Natürlichen Pflanzenfamilien, Aufl. 2, 19C. Englemann, Leipzig.

Rauh, W. 1967. Die Grossartige Welt der Sukkulenten. Parey, Hamburg and Berlin.

White, A., R. A. Dyer & B. L. Sloane. 1941. The Succulent Euphorbieae, Southern Africa. Abbey Garden Press, Pasadena.

PHYTOCHEMISTRY AND SYSTEMATICS OF THE EUPHORBIACEAE[1]

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ABSTRACT

Phytochemical data provide much useful information concerning relationships both within the Euphorbiaceae and between that family and putative relatives. Within the Euphorbiaceae, the presence of several groups of secondary metabolites support certain infrafamilial groupings, whereas data related to the biosynthesis and distribution of other secondary metabolites provide information concerning the relationship of the Euphorbiaceae to other families. Similarities in chemistry to both the Geraniales and Malvales are found, supporting the suggestion by Webster (1987) that the differences between the Dilliniidae and Rosidae may not be as great as previously thought, and that the Euphorbiaceae may have arisen from ancestors intermediate to those two groups.

The chemistry of the Euphorbiaceae is among the most diverse and interesting of flowering plant families (Evans, 1986a, b; Hegnauer, 1966b, 1989) and is comparable to the biological diversity of the family (Radcliffe-Smith, 1986; Webster, 1987). Because of the presence of unusual secondary metabolites, many species of euphorbiaceous plants are poisonous and have been involved in human and livestock poisoning. Plants of this family, especially those of the genus *Euphorbia*, are known for their ability to induce dermatitis (Evans & Schmidt, 1980). Others have been used in folk medicine, as piscicides, or as arrow poisons. Several euphorbs are important food plants, and a number are important economically as ornamental plants and as sources of rubber, chemical precursors, lubricants, and medicinal compounds (Radcliffe-Smith, 1986; Rizk, 1987).

The principal goal of this article is to evaluate systematic and evolutionary relationships in the Euphorbiaceae with information derived from extant phytochemical literature. These data point to certain affinities of the Euphorbiaceae and suggest alignments of subfamilial taxa of this enigmatic family as well.

What types of secondary compound data are likely to be useful? Both the presence and absence of secondary metabolites and the biosynthetic pathways responsible for their production are useful for establishing taxonomic and phylogenetic relationships. The products of relatively short pathways beginning with readily available precursors are more likely to have originated several times and usually are widespread among higher plants. Examples are glycosides of the flavones apigenin and luteolin and the flavonols kaempferol and quercetin (Seigler, 1977, 1981b). In general, compounds that are formed via complicated pathways with many steps are less likely to have evolved than those from simple pathways with fewer steps. In deliberations of this sort, one almost must consider the precursors that may be present in a particular plant. Although all diterpenes are of relatively complex biosynthetic origin, many are derived from kaurene, a precursor of gibberellins in plants. Because gibberellins are universal in plants, kaurene, and the biosynthetic pathways leading to kaurene, presumably occur in all plants. Thus, many apparently complex diterpenes actually arise via relatively short modifications of ubiquitous biosynthetic pathways. Examples include compounds such as (-)-kaurene, a diterpene found in several euphorbiaceous taxa.

However, cocarcinogenic diterpenes, found only in the Euphorbiaceae and Thymelaeaceae, are derived from complicated pathways involving numerous steps not shared with other biosynthetic pathways. The probability that the pathways leading to these compounds have evolved more than once is slight, and, hence, the probability that plants that possess these compounds are related is great.

Understanding phylogenetic relationships of the Euphorbiaceae is made difficult by the large number of both morphological and chemical autapomorphic characters. Many exotic and interesting compounds occur in a single species or group of species (Hegnauer, 1989; Rizk, 1987).

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Thousands of compounds from many different chemical classes have been reported from members of the Euphorbiaceae. This article makes no attempt to review the literature exhaustively; references are to recent and readily available review articles rather than to the original works. Readers should consult the references cited in these reviews for more detailed information. A predominance of chemical work concerns the large genus *Euphorbia*, which has been studied in greater detail than most other representatives of the family.

Although the chemistry is doubtful in some instances, a more usual problem involves the uncertain identity of the plant materials used. Voucher specimens were not maintained in many older and some present-day studies. In other instances, the identification of the plant material was not verified by a specialist; this is especially important for the Euphorbiaceae.

Major Types of Secondary Metabolites in the Euphorbiaceae

Of all chemical classes, the most useful for chemotaxonomic study of the Euphorbiaceae above the level of genus appear to be alkaloids, cyanogenic glycosides, diterpenes, glucosinolates, seed and other lipids, tannins, and triterpenes (Hegnauer, 1966b, 1989). These are useful for several reasons. Alkaloids, diterpenes, tannins, and triterpenes arise from complex pathways; the products have limited distribution within the Euphorbiaceae. Cyanogenic glycosides and glucosinolates arise from pathways of intermediate complexity; although these compounds and the pathways leading to them are found in other plant families, the distribution of these glycosides is restricted within the Euphorbiaceae. Both cyanogenic glycosides and glucosinolates provide useful characters for recognition of subgroups within the family. Other compounds, such as amino acids, coumarins, flavonoids, lignans, monoterpenes, and sesquiterpenes, are widely distributed among many higher plant groups and within the Euphorbiaceae. Although not sufficiently distinctive or restricted in distribution to be useful at the family or subfamily level, these compounds may serve as useful characters at lower taxonomic levels.

Alkaloids

Alkaloids are widely distributed in plants. These nitrogenous compounds range from very simple, and usually widespread, to highly complex entities of restricted distribution. Both types are found in the Euphorbiaceae. The use of alkaloids for chemosystematic purposes in the Euphorbiaceae previously has been reviewed (Hegnauer, 1963, 1966a, b, 1989; Seigler, 1977).

Among the relatively simple and widespread alkaloids are the harmane types, such as L-3-carboxy-1,2,3,4-tetrahydrocarboline (**1**),[3] found in the seeds of *Aleurites fordii* Hemsl. (Crotonoideae: Aleuritidae: Aleuritinae) (Okuda et al., 1975), and N_β-methyltetrahydroharman (**2**) isolated from *Spathiostemon javensis* Blume (*Homonoia riparia* (Blume) Müll. Arg.) (Acalyphoideae: Acalypheae: Lasiococcinae) (Johns et al., 1970). An ester of vasicine (**3**) (a pyrroloquinazoline alkaloid) has been reported from *Croton draco* Schltdl. (Crotonoideae: Crotoneae), but some uncertainty exists about the identity of the plant material (Hegnauer, 1966a, b; Rizk, 1987). Several piperidine alkaloids have been reported from members of the Euphorbiaceae. Among these are astrocasine (**4**) [*Astrocasia tremula* (Griseb.) Webster (syn. *Astrocasia phyllanthoides* C. B. Rob. & Millsp.) Phyllanthoideae: Phyllantheae: Astrocasiinae], 2,4-dimethoxy-Ψ,Ψ-dimethylallyl-*E*-cinnamoylpiperidide (**5**) (*Excoecaria agallocha* L. Euphorbioideae: Hippomaneae: Hippomaninae), and julocrotine (**6**) (*Julocroton* spp.; this genus is only weakly separated from *Croton*) (Rizk, 1987). Hordenine (**7**) is found in *Flueggea virosa* (Willd.) Baill. (syn. *Securinega virosa* (Willd.) Pax & Hoffm.) (Phyllanthoideae: Securineginae) (Hegnauer, 1966b). Pyrrolidine and tropane alkaloids have been reported from *Margaritaria discoideus* (Baill.) Webster (syn. *Phyllanthus discoideus* Müll. Arg.) (Phyllanthoideae: Flueggeinae) (phyllalbine) and *Croton gabouga* S. Moore [4-hydroxyhygrinic acid (**7**)] (Rizk, 1987; Seigler, 1977). An unusual type of quinolizidine alkaloid (**8**) occurs in *Poranthera corymbosa* Brongn. (Phyllanthoideae: Andrachneae: Porantherinae). This series of alkaloids is biosynthetically related to piperidine alkaloids (Howard & Michael, 1986). The hypotensive principle of *Jatropha podagrica* Hook. (Crotonoideae: Jatropheae) is tetramethylpyrazine (**9**), a compound also known from members of the Solanaceae and Asclepiadaceae (Nahrstedt, 1982). Purine alkaloids occur in *Cnidoscolus basiacanthus* (Pax & K. Hoffm.) Macbride (syn. *Jatropha basiacantha* Pax & K. Hoffm.) (Rizk, 1987). A questionable report of physostigmine (*Hippomane mancinella* L., Euphorbioideae: Hippomaneae: Hippomaninae) should be confirmed (Lauter & Foote, 1955).

Imidazole alkaloids have been isolated from the

[3] See figure at the end of the article.

genera *Glochidion* (Phyllanthoideae: Phyllantheae: Flueggeinae) and *Alchornea* (Acalyphoideae: Alchornieae: Alchorneinae) (Johns & Lamberton, 1967; Maat & Beyerman, 1983; Rizk, 1987). A series of imidazole alkaloids including N^{α}-cinnamoylhistamine (**15**), N^{α}-oxodecanoylhistamine (**10**), glochidicine (**11**), and glochidine (**12**) occur in *Glochidion philippicum* (Cav.) C. B. Rob. (Rizk, 1987). Alkaloids with this general structure are known from several other groups of plants (Acanthaceae, Cactaceae, Fabaceae, Orchidaceae, and Rutaceae), but the structures are so diverse that the alkaloids may be of distinct biosynthetic origin (Seigler, 1977).

The pyrimidine and guanidine alkaloids of *Alchornea* contain a hemiterpene unit and also represent an unusual structural type. Among the pyrimidine alkaloids of *Alchornea javanensis* Müll. Arg. are alchornidine (**13**) and alchornine (**14**). This plant also contains N^1,N^2-diisopentenylguanidine and N^1,N^2,N^3-triisopentenylguanidine (Hegnauer, 1989; Rizk, 1987).

Because of the widespread occurrence of the above alkaloids among other plants (probably reflecting the ease with which they can arise), and/or their sporadic distribution among the Euphorbiaceae, their presence does not suggest or confirm familial or subfamilial relationships. However, other genera related to *Glochidion* and *Alchornea* should be examined for the presence of imidazole, pyrimidine and guanidine alkaloids, respectively, as these compounds could provide useful characters at the specific and generic level.

In contrast, the distribution of benzylisoquinoline alkaloids is restricted among higher plants. Most occur in certain families of the Magnoliales and Ranunculales, although sporadic occurrences are known from other plant groups. Benzylisoquinoline alkaloids are common in the following families: Annonaceae, Aristolochiaceae, Berberidaceae, Eupomatiaceae, Hernandiaceae, Fumariaceae, Lauraceae, Magnoliaceae, Menispermaceae, Monimiaceae, Nelumbonaceae, Papaveraceae, Ranunculaceae, and Winteraceae. Alkaloids of this structural type are found less commonly in other families including the Euphorbiaceae (*Croton*, *Andrachne*), Fabaceae (*Erythrina*), Rhamnaceae (*Rhamnus*, *Phylica*, *Colletia*, *Colubrina*, *Discaria*, *Ratanilla*, *Talguenea*, and *Zizyphus*), Phellinaceae (*Phelline*), Symplocaceae (*Symplocos*), Rutaceae, Araliaceae (*Hedera*), Apiaceae (*Heracleum*), Caprifoliaceae (*Symphoricarpos*), Rubiaceae (*Cephaelis*), and Araceae (*Lysichiton*) (Bisset, 1985; Dahlgren et al., 1981).

In the Euphorbiaceae, aporphine (thaliporphine and glaucine), proaporphine, dihydroproaporphine, and morphinandienone types of benzylisoquinoline alkaloids have been isolated from *Croton* species (Rizk, 1987; Rizk & El-Missiry, 1986). Among the individual alkaloids isolated are glaucine (**16**), orotonsine, pronuciforine, sparsiflorine (**17**), thaliporphine, crotsparine (**18**), *N*,*O*-crotsparine, *N*-methylcrotsparine, crotonosine (**19**), flavinantine, flavinine, linearisine (**20**), 3-methoxy-4,6-dihydroxymorphinandien-7-one, *N*-norsalutaridine, norsinoacutine, salutaridine (**21**), and salutarine (Rizk, 1987). Salutaridine was first discovered in *Croton salutaris* Casar. from Brazil and later found in low concentrations in *Papaver somniferum* L., where it is an intermediate in the biosynthesis of morphine alkaloids. Bisbenzylisoquinoline alkaloids have been reported from *Andrachne cordifolia* (Decne.) Müll. Arg. (Phyllanthoideae: Andrachneae: Andrachninae) (Khan et al., 1983).

The securinine alkaloids are a small group of compounds produced only by members of the subfamily Phyllanthoideae. Among these, allosecurinine (**22**), dihydrosecurinine, norsecurinine (**23**), phyllantidine, phyllantine, phyllochrysine, securinine (**24**), suffruticosine, and virosecurinine (**25**) come from *Securinega*, *Phyllanthus*, and *Flueggea* (Phyllantheae: Flueggeinae) species. Securinine and related alkaloids are synthesized from lysine and tyrosine via a unique pathway and represent a novel type of alkaloids not found in other plant groups (Beutler & Brubaker, 1987; Rizk, 1987; Seigler, 1977). Their presence in several members of the Phyllanthoideae reinforces the close relationship of the genera *Phyllanthus*, *Flueggea*, and *Securinega*.

Ricinine (**26**) (*Ricinus communis* L., Acalyphoideae: Acalypheae: Ricininae), nudiflorine (**27**), ricinidine (**28**), methyl-3-carboxamide-6-pyridone (*Trewia* spp., Acalyphoideae), and mallorepine (**29**) (*Mallotus*, Acalyphoideae; Acalypheae: Rottlerinae) all appear to be closely related and are probably derived from nicotinic acid (Fodor & Colosanti, 1985; Sastry & Waller, 1972; Strunz & Findlay, 1985; Waller & Nowacki, 1978). The structures of these alkaloids suggest a similar biosynthetic origin from nicotinic acid as is probably true for the cyanogenic glycoside acalyphin (**30**) (*Acalypha indica* L., Acalyphoideae: Acalypheae: Acalyphinae) (Nahrstedt, 1987).

Maytansinoid alkaloids, such as trewiasine (**31**) are reported often from plants of the genera *Maytenus* and *Putterlickia* of the Celastraceae and *Colubrina* of the Rhamnaceae (Reider & Roland, 1984), but also have been encountered in the genus *Trewia* (Powell et al., 1981, 1983).

Peptide alkaloids are known from *Hymenocardia acida* Tul. (Phyllanthoideae: Hymenocardieae) (Pais et al., 1967; Seigler, 1977). Similar alkaloids, such as hymenocardine (**32**) have been isolated from *Panda* of the Pandaceae, which Webster (1994) now merges with the Euphorbiaceae. This merger is supported by peptide alkaloid chemical data. Peptide alkaloids also have been isolated from the Celastraceae, Menispermaceae (*Cocculus*), Rhamnaceae, Rubiaceae, Sterculiaceae (*Melochia* and *Waltheria*), and Urticaceae (Schmidt et al., 1985).

CYANOGENIC GLYCOSIDES

Plants from subfamilies Phyllanthoideae, Crotonoideae, and Acalyphoideae of the Euphorbiaceae contain glycosides capable of releasing cyanide upon hydrolysis. This property also has been reported, but not confirmed, from plants of the Euphorbioideae. The cyanogenic glycosides involved are derived from several different precursors, and although one compound of this type, acalyphin (**30**), is found only in the Euphorbiaceae, others are widely distributed.

Several species of the subfamily Phyllanthoideae are cyanogenic. Among these are *Andrachne colchica* W. Fisch. & E. Meyer*, *A. decaisnei* Benth., *A. telephioides* L.*, *Breynia obtusiflora*, *Bridelia cathartica* G. Bertol. *, *B. exaltata* F. Muell., *B. duvigneaudii* J. Léonard, *B. mollis* Hutch., *B. monoica* Merr.*, *B. ovata* Decne., *B. pervilleana* Baill., *B. scleroneura* Müll. Arg.*, *B. tomentosa* Blume, *Phyllanthus acuminatus* Vahl., *P. angustifolius* (Sw.) Sw., *P. gasstroemii* Müll. Arg., *P. lacunarius* F. Muell., *P. speciosus* Jacq., *Poranthera microphylla* Brongn.*, *P. corymbosa*, *Flueggea suffruticosa* (Pall.) Baill.* [syn. *Securinega suffruticosa* (Pall.) Rehder, *S. ramiflora* Müll. Arg., and *S. flueggeoides* Müll. Arg.] (van Valen, 1978). Those species marked with an * are known to contain triglochinin (**33**) as the cyanogenic glycoside; other species are known to be cyanogenic, but the compounds have not been characterized. Plants of *Phyllanthus gasstroemii* contain taxiphyllin (**34**). Plants of *Bridelia monoica* contain dhurrin (an enantiomer of taxiphyllin) and triglochinin (Hegnauer, 1989; van Valen, 1978), but no other cyanogens have been substantiated from species of this subfamily (Bridelieae). All three cyanogens are derived from tyrosine.

A number of species of the subfamily Crotonoideae are known to be cyanogenic. Among these are *Aleurites trisperma* Blanco, *Beyeria lescheenaultii* (DC.) Baill. and *B. viscosa* (Labill.) Miq. (Ricinocarpeae: Ricinocarpinae), several species of *Cnidoscolus*‡ (Manihoteae), *Croton lobatus* L., *C. punctatus* Lour., *C. scouleri* Hook. f., *Elaeriospermum tapos* Blume (Elatiospermeae), several *Hevea*‡ species (Micrandreae: Heveinae), many species of *Manihot* (*Manihot esculenta* Crantz‡) (Manihoteae), (Adsersen et al., 1987; Hegnauer, 1989; van Valen, 1978). Weakly positive tests have been observed with some species of the genus *Jatropha* (e.g., *J. capensis* Sond.). Most of the species examined in this subfamily contain linamarin (**35**) and usually smaller amounts of lotaustralin (**36**) (species marked with a ‡). In addition, careful examination of the cyanogens of *Hevea brasiliensis* Müll. Arg. (Crotonoideae: Micrandreae: Heveinae) revealed the presence of the corresponding diglycoside, linustatin (**37**) (Lieberei, 1986, 1988). In general, lines of *Hevea brasiliensis* with large amounts of cyanogenic glycosides and β-glycosidases are the most susceptible to the South American leaf blight (Lieberei, 1988). Cyanogenic diglycosides, such as linustatin, appear to be involved in transport of cyanogenic glycosides within the plants and are probably more widely distributed than realized (Lieberei et al., 1985).

Several species from the Acalyphoideae also are known to be cyanogenic. Among these are *Acalypha indica* L., *A. ostryaefolia* Riddell, *Dalechampia micromeria* Baill. (Plukenetieae: Dalechampiinae), *Mercurialis annua* L. (Acalypheae: Mercurialinae), and *Ricinus communis* (Hegnauer, 1989; Nahrstedt, 1987; van Valen, 1978). The cyanogenic glycoside acalyphin (**30**) has been isolated from *Acalypha indica* (Nahrstedt, 1987).

A number of plants of the subfamily Euphorbioideae have been reported to be cyanogenic. Among these are *Chamaesyce abdita* Burch, *C. galapageia* (B. L. Rob. & Greenm.) Burch, *C. hirta* (L.) Millsp. (*Euphorbia hirta* L.), *C. maculata* (L.) Small [*C. supina* (Raf.) Moldenke], *C. recurva* (Hook. f.) Burch, *C. thymifolia* (L.) Millsp. (*Euphorbia thymifolia* L.), *C. viminea* (Hook. f.) Burch (Euphorbieae: Euphorbiinae), *Euphorbia drummondii* Boiss. [probably *E. boophthona* C. A. Gardner and *E. clutioides* (G. Forst.) C. A. Gardner], *E. eylesii* Rendle, *E. hexagona* Nutt., *E. lupatensis* N. E. Br. (Euphorbieae: Euphorbiinae), *Gymnanthes lucida* Sw. (Hippomaneae: Hippomaninae), *Sapium haematospermum* Müll. Arg., *S. sebiferum* (L.) Roxb. (Hippomaneae: Hippomaninae), *Stillingia dentata* (Torr.) Britton & Rusby, *S. sanguinolenta* Müll. Arg. (Hippomaneae: Hippomaninae), and doubtfully *Colliguaja integerrima* Gillies & Hook. (Hippomaneae: Hip-

pomaninae) (Hegnauer, 1989). To date, the cyanogenic compounds of the Euphorbioideae have not been characterized.

DITERPENES

A large variety of diterpenes occur in the Euphorbiaceae (Hegnauer, 1966b, 1989). These may be grouped into compounds derived from monocyclic precursors and their derivatives (including cocarcinogenic diterpenes), kaurene and related compounds, and labdane derivatives.

Simple diterpenes from geranylgeranyl pyrophosphate. Geranylgeraniol derivatives are found in several species of *Croton*, e.g., *C. kerrii* Airy Shaw and *C. sublyratus* Kurz. (Hegnauer, 1989). One simple diterpene, 18-hydroxy-6-*cis*-geranylgeraniol (**38**) from *Croton kerrii* stems, appears to serve as a prostaglandin analogue. This compound protects the digestive tract from the effects of ulceration and promotes wound healing (Croteau & Johnson, 1985; Sato et al., 1980).

Cyclic diterpenes from geranylgeranyl pyrophosphate. Cembrene (**39**), duvatrienediols (such as **40**), and a large series of compounds of the Euphorbiaceae (the lathyrols, casbene, jatrophanes, rhamnifolanes, and crotofolanes, as well as the cocarcinogenic tiglianes, daphnanes, and ingenanes) are derived from cyclization of a geranylgeranyl pyrophosphate precursor to a large monocyclic system (Schmidt, 1987). Casbene (**41**), a bicyclic 14-membered ring compound, is a phytoalexin in *Ricinus communis*. This compound appears to be derived from head-to-tail condensation of the diterpene pyrophosphate precursor, geranylgeranyl pyrophosphate (GGPP) (Schmidt, 1987). A compound with related structure has been isolated from *Croton nitens* Sw.

Several unusual structural types of diterpenes derived from monocyclic precursors occur in the Euphorbiaceae. Jatrophanes (such as **42**) are known from *Jatropha gossypiifolia* L., *J. macrorhiza* Benth., *Euphorbia characias* L., *Euphorbia esula* L., *E. maddenii* Boiss., *E. helioscopia* L., and *E. kansui* Liou ex H. B. Ho (Hegnauer, 1989; Manners, 1987; Schmidt, 1987). Rhamnifolanes (**43**) are known from *Croton rhamnifolius* Kunth. (Schmidt, 1987). Lathyranes (such as **44**) are known from *Bertya cupressoidea* Airy Shaw (Crotonoideae: Ricinocarpeae: Bertyinae), *Euphorbia helioscopia* L. *Euphorbia characias, E. ingens* E. Meyer, *E. jolkini* Boiss., *E. lathyris* L., and *Macaranga tanarius* Müll. Arg. (Acalyphoideae: Acalypheae: Macaranginae) (Hegnauer, 1989; Schmidt, 1987). Crotifolanes (such as **45**) are known from *Croton corylifolius* Lam. (Schmidt, 1987).

Cocarcinogenic diterpenes. The powerful purgative properties of "croton oil," the seed oil of *Croton tiglium* L. (native to Southeast Asia), have long been known. The active compounds have been isolated and shown to consist of the 12,13-diesters of a tetracyclic diterpene, phorbol (**46**) (Hecker & Schmidt, 1974). These compounds are potent irritants and cocarcinogens (Evans & Schmidt, 1980; Evans & Soper, 1978; Hecker, 1977, 1986; Kinghorn, 1979). These compounds are called cocarcinogens or tumor promoters because they are not directly carcinogenic, but application of a carcinogen following contact with cocarcinogenic diterpenes results in greatly enhanced carcinogenic activity. At the same time, these compounds have been examined for their antitumor properties (Evans & Soper, 1978; Hecker, 1986).

Biosynthetically, these compounds are derived from monocyclic diterpenoid precursors and are biosynthetically related to casbene, the lathyranes, and the jatrophanes. Several major structural types are found. Most important among these types are the ingenane (such as **47**) (Schmidt, 1986b), daphnane (**48**) (Schmidt, 1986a), and tigliane (**46**) (Evans, 1986a, b) series. Precursors of the tiglianes, ingenanes, and daphnane type cocarcinogenic diterpenes have been isolated from the Euphorbiaceae as well as Thymelaeaceae.

Tiglianes (e.g., phorbol) (tetracyclic with a six- and a seven-membered ring) occur in *Aquilaria, Daphnopsis, Pimelea* (Thymelaeaceae) as well as *Aleurites, Croton* (Crotonoideae), *Euphorbia, Hippomane, Sapium*, and *Synadenium* (Euphorbioideae: Euphorbieae: Euphorbiinae) (Bagavathi et al., 1988; Hecker, 1977; Evans & Soper, 1978; Schmidt, 1986c).

Ingenanes (e.g., ingenol) (tetracyclic with two seven-membered rings) occur in *Euphorbia* (and *Elaeophorbia*, considered a synonym of *Euphorbia* by Webster, 1975, 1994) species (Hecker, 1977; Evans & Soper, 1978), but not in other taxa of the Euphorbiaceae and Thymelaeaceae that were examined (Hecker, 1977).

Daphnane compounds (e.g., daphnetoxin) (tricyclic) occur in both the Euphorbiaceae [*Baliospermum* (Crotonoideae: Codiaeae), *Cunuria* (Crotonoideae: Micrandreae: Micrandrinae), *Euphorbia, Excoecaria, Hippomane, Hura* (Euphorbioideae: Hureae), and *Stillingia*] and the Thymelaeaceae (*Daphne, Daphnopsis, Diarthron, Dirca, Gnidia, Lasiosiphon, Pimelea, Synaptolepis, Thymelaea,*

and *Wikstroemia*) (Adolf et al., 1988; Hecker, 1977; Powell et al., 1985; Schmidt, 1986c). Daphnanes are probably derived from tiglianes by opening of the cyclopropane ring (Evans & Soper, 1978).

Within the genus *Euphorbia*, subgenera *Chamaesyce* and *Poinsettia* lack cocarcinogenic diterpenes. Both tiglianes and ingenanes are common in subgenera *Euphorbia* and *Tithymalus* (Evans & Kinghorn, 1977; Evans & Soper, 1978).

Determination of active diterpenes by means of a 3H-PDBU (tritiated phorbol receptor binding assay) suggested their presence in several previously untested samples of euphorbiaceous plants. Activity was observed in the Phyllanthoideae [*Antidesma* (Antidesmeae: Antidesminae), *Drypetes* (Drypeteae), *Glochidion*, and *Uapaca* (Uapaceae)], although only that observed in *Antidesma* was strongly positive (Beutler et al., 1989). Cleistanthol, a cocarcinogenic diterpene, is found in *Cleistanthus schlechteri* Hutch. (Phyllanthoideae: Bridelieae) (McGarry et al., 1971). Only weak activity was observed in the Acalyphoideae (*Alchornea* and *Trewia*) and none from the Oldfieldioideae. Among the Crotonoideae, activity was found in *Cnidoscolus*, *Jatropha*, *Ricinodendron* (Aleuritidae: Ricinodendrinae), *Codiaeum*, *Dimorphocalyx*, *Fahrenheitia* (Codiaeae), *Aleurites*, *Crotonogyne* (Neoboutonieae: Crotonogyninae), *Cyrtogonone* (Neoboutonieae: Crotonogyninae), *Croton* (including *Eremocarpus*) (Crotoneae) (Beutler et al., 1989). Similar activity was observed in *Aleurites fordii* (Aleuritidae: Aleuritinae) (Schmidt, 1987). In the Euphorbioideae, activity was found in *Plagiostyles* (Stomatocalyceae: Stomatocalycinae), *Homalanthus* (Hippomaneae: Carumbiinae), *Duvigneaudia* (Hippomaneae: Hippomaninae), *Excoecaria*, *Hippomane*, *Maprounea* (Hippomaneae: Hippomaninae), *Sapium*, and *Stillingia* (Beutler et al., 1989). A large number of other genera were examined and found to lack this activity.

Diterpenes derived from kaurene. Kaurene (**49**) is probably found in all plants as it is a precursor for gibberellins, although usually only in small amounts. Structurally related compounds are accumulated in a number of euphorbiaceous taxa. For example, *ent*-3β-hydroxybeyer-15(16)-ene-2,12-dione (**50**) is known from *Androstachys johnsonii* Prain (Oldfieldioideae: Picrodendreae: Androstachydeae) (Pegel et al., 1971), *Beyeria leschenaultii* (DC.) Baill., and *B. calycina* Airy Shaw (Bakker et al., 1972; Ghisalberti et al., 1978).

Many pimarane and abietane derivatives are found in the Asteraceae, Lamiaceae, Euphorbiaceae, and the genus *Jungermannia* (a bryophyte) (Croteau & Johnson, 1985). These compounds occur in the leaf-surface resins of members of the tribe Ricinocarpoideae (Croteau & Johnson, 1985; Dell & McComb, 1974).

Oxygenated diterpene derivatives. A number of highly oxygenated diterpenes based on the labdane skeleton are found in the families Asteraceae, Euphorbiaceae, Lamiaceae, and Verbenaceae (Croteau & Johnson, 1985; Seigler, 1981a). These compounds are complex and restricted in distribution. In the Euphorbiaceae, they are primarily found in the genus *Croton* (Seigler, 1981a). Furan formation between C-15 and C-16 is common. Such compounds are cordylifoline (Burke et al., 1976) and isocrotocaudin (**51**). At least two diterpenes of this type are found in *Croton setigerus* Hook. [*Eremocarpus setigerus* (Hook.) Benth.] (Bajaj et al., 1986; Jolad et al., 1982), and another compound, mallotucin A, isolated from *Mallotus repandus* (Willd.) Müll. Arg. has been shown identical to teucrin (**52**) [originally isolated from *Teucrium* (Lamiaceae)] (Kawashima et al., 1976).

GLUCOSINOLATES

Glucosinolates in the Euphorbiaceae are confined to a small number of taxa. Most important among these are *Drypetes gossweileri* S. Moore and *Putranjiva roxburghii* Wall. (Phyllanthoideae: Drypeteae). *Putranjiva* is merged with *Drypetes* by some (Hurusawa, 1954). Glucoputranjivin (**53**), glucococh learin (**54**), and glucojaputin have been isolated from *Putranjiva roxburghii* (Rizk, 1987). Although glucosinolates are derived from the same pathways as cyanogenic glycosides, glucosinolates of the Euphorbiaceae are based on aliphatic aglycones and do not resemble the cyanogenic glycosides of this subfamily. Benzyl isothiocyanate has been reported from the latex of *Jatropha multifida* L. (Rizk & El-Missiry, 1986).

Among higher plants, the distribution of glucosinolates is restricted to a small number of families (Rodman, 1991a, b; Rodman et al., 1993). One group of families includes the Brassicaceae, Capparidaceae, Resedaceae, and Tovariaceae. A number of other enigmatic glucosinolate-containing families appear to be related to those families. Several other glucosinolate-containing families may be related to each other, but the glucosinolate-containing members of the Euphorbiaceae do not appear to be closely related to any other glucosinolate-containing plants (Hegnauer, 1966b; Rodman, 1991a, b; Rodman et al., 1993).

SEED AND OTHER LIPIDS

A number of unusual fatty acids occur primarily as components of seed lipids of members of the Euphorbiaceae but are occasionally found in the lipids associated with other plant parts (Smith, 1970). Many of these involve unusual sites of unsaturation and *E* double bonds. For example, *Sapium sebiferum* (L.) Roxb. contains decanoic acid with 2-*E*-4-*Z* unsaturation (**55**) and *Sebastiana ligustrina* (Michx.) Müll. Arg. contains dodeca-2,4-dienoic acid (**56**) (Smith, 1970). A decanoic acid with a cyclopropane ring (**57**) has been isolated from *Croton* species (Hegnauer, 1989).

α-Eleostearic acid (**58**) is found in tung oil (*Aleurites fordii*, *A. montana* (Lour.) E. H. Wilson, *A. remyi* Sherff., and *A. trisperma*, but only questionably from the seed oil of *A. moluccana* Willd.). This rapidly polymerizing acid is also found in the oil of *Garcia nutans* Rohr., *Ricinodendron viticoides* Mildbr., and *R. rautanenii* Schinz. (Crotonoideae: Aleuritidae: Ricinodendrinae), (Hegnauer, 1989; Jacobson et al., 1981; Smith, 1970).

An unusual glyceride containing an allenic linkage and a short chain hydroxy acid (**59**) is found in the seed lipids of *Sapium sebiferum*, *Stillingia sylvatica* L., *Stillingia texana* I. M. Johnst., and *Sebastiana ligustrina* (Michx.) Müll. Arg. (Hegnauer, 1989; Heimermann & Holman, 1972).

Various hydroxy acids also occur. Although found in other plants and microorganisms (for example, in fungi of the genus *Claviceps*), ricinoleic acid (**60**) is the major fatty acid of the triglycerides of *Ricinus communis*. *Securinega suffruticosa* seed oil contains 12-hydroxyheptadecanoic (**61**) and 12-hydroxyeicosanoic acids (Hegnauer, 1989). The main constituent of the seed oil of *Mallotus philippensis* (Lam.) Müll. Arg. and *Trewia nudiflora* L. is 18-hydroxyoctadec-*Z*-9-*E*-11-*E*-13-trienoic (α-kamolenic) acid (**62**) (Calderwood & Gunstone, 1953; Hegnauer, 1989).

Epoxy fatty acids are found in *Alchornea cordifolia* Müll. Arg. [a rich source of (+)-*Z*-14,15-epoxy-*Z*-11-eicosenoic acid (**63**)] (Kleiman et al., 1977), *Cephalocroton cordofanus* Hochst. (Acalyphoideae: Epiprineae: Epiprinineae) (Bharucha & Gunstone, 1956), and *Euphorbia lagascae* Spreng. (vernolic or *cis*-12,13-epoxyoleic acid) (**64**) (Kleiman et al., 1965; Smith, 1970). The furanoid compound, 10,13-epoxy-11-methyloctadeca-10,12-dienoic acid (**65**), occurs in the latex of *Hevea brasiliensis* (A. Juss.) Müll. Arg. (Hasma & Subramaniam, 1978).

Dihydroxy fatty acids are found commonly in the Euphorbiaceae as well as in several other families. These compounds are thought to be derived biosynthetically from epoxy fatty acids. 9,14-dihydroxyoctadecadien-10,12-oic acid (**67**) and *erythro*-9,10-dihydroxy-1-octadecanyl acetate (**66**) are found in the seeds of *Aleurites fordii* and 11,13-dihydroxy-9-*trans*-tetracosenoic acid in *Baliospermum axillare* Blume (Hegnauer, 1989).

TANNINS

Polyphenolic compounds known as tannins are especially widespread among woody plants, but also are found in herbaceous species. Both hydrolyzable and condensed tannins are found in plants from the Euphorbiaceae (Rizk & El-Missiry, 1986). Hydrolyzable tannins that yield ellagic acid (**68**) on hydrolysis have been reported from several species, primarily from the genus *Euphorbia* (Rizk & El-Missiry, 1986). One specific ellagitannin, geraniin (**69**), is widespread in the family and has been isolated from members of the Acalyphoideae, Crotonoideae, Euphorbioideae, and Phyllanthoideae (Hegnauer, 1989; Okuda et al., 1980). In the first three of these subfamilies, it is accompanied by the rarely encountered compound mallotusic acid (**70**). Geraniin is especially common in the Geraniaceae, but absent from the Myrtaceae, Fagaceae, and Fabaceae. Tannins with quite distinctive structures have been isolated from euphorbiaceous plants, especially from the genus *Euphorbia* (Okuda et al., 1980).

Because tannins have complex structures and in some cases appear to have restricted distribution, these compounds should be useful for systematic studies. Unfortunately, tannins occur in complex mixtures; this complexity has precluded analysis in many cases. Tannin content alone is not useful for taxonomic purposes. Future work may clarify the structures of many of these compounds and provide additional chemosystematic markers for analysis of plant groups.

TRITERPENES

Many plants of the Euphorbiaceae possess latex that is rich in terpenes. Triterpenes are predominant in these terpenoid fractions in most species. Reviews of triterpenes (Das & Mahato, 1983; Hegnauer, 1989; Ourisson et al., 1979; Pant & Rastogi, 1979; Rizk & El-Missiry, 1986; Seigler, 1981a) include many references to the Euphorbiaceae. Species of triterpenes from the genus *Euphorbia* easily outnumber those of all other euphorbiaceous taxa (Hegnauer, 1989; Ourisson et al., 1979; Ponsinet et al., 1968; Ponsinet & Ourisson, 1965).

Most of the triterpenes that have been reported from the Euphorbiaceae (e.g., β-sitosterol, α- and β-amyrin (**71**), friedelan, taraxerol, lupeol (**72**),

cycloartenol (**73**), taraxerone, β-amyrin acetate, pseudotaraxasterol, betulin, taraxerone, 24-methylenecycloartenol, taraxasterol, friedilin, oleanolic and ursolic acid, and butyrospermol) are widespread among higher plants and are of little value for establishing taxonomic relationships at higher levels. Their presence may, however, be useful taxonomically at the species or subgeneric level (Mahlberg et al., 1988). Because triterpenes are difficult to isolate, purify, and characterize, many older reports (for example, those for lanosterol) should be re-examined.

Euphol (**74**), tirucallol (**75**), and euphorbol (**76**) often are found in the latex of members of the genus *Euphorbia* (Rizk & El-Missiry, 1986). In addition, euphol is found in the Burseraceae, Rutaceae, Simaroubaceae, Cneoraceae, and Meliaceae, and tirucallol in the Anacardiaceae; either (or both) serve as precursors for a series of metabolically altered triterpenes in the Cneoraceae, Meliaceae, Rutaceae, and Simaroubaceae.

Hundreds of *Euphorbia* species have been examined for triterpene content. The major triterpenes present are compounds related to cycloartenol, tetracyclic triterpenes, and pentacyclic triterpenes (Hegnauer, 1989; Ourisson et al., 1979). Bauerenol (**77**), germanicol (**78**), and phyllanthol (**79**) are pentacyclic triterpenes found in many plants from the genus *Euphorbia* (Rizk & El-Missiry, 1986). In general, herbaceous species accumulate cycloartenol, cactuslike species accumulate euphol and euphorbol, whereas "coral-like species" accumulate euphol and tirucallol (Ponsinet et al., 1968; Ourisson et al., 1979; Ramaiah et al., 1979; Rizk & El-Missiry, 1986). Members of the American subgenus *Poinsettia* usually contain fatty acid esters of pentacyclic triterpenes (Hegnauer, 1989; Ourisson et al., 1979). Although cholesterol is normally a minor plant sterol, in *Euphorbia pulcherrima* Willd. this compound comprises almost half the sterol mixture (Rizk & El-Missiry, 1986).

There have been too few other investigations to apply the data effectively, but probably plants of most other euphorbiaceous genera do not accumulate triterpenes to the same extent as do species of *Euphorbia*.

A number of new and distinctive compounds (primarily pentacyclic triterpenes related to lupeol) have been reported from the genus *Glochidion* (Hegnauer, 1989; Rizk & El-Missiry, 1986).

Cardiac glycosides (such as **80**), another group of triterpenoid derived compounds sporadically distributed among plants, are found in several members of the genus *Mallotus* (Rizk, 1987; Roberts et al., 1966).

Cucurbitacins (such as **81**) have been reported from the Phyllanthoideae [*Antidesma rupicola* Wedd., *Cleistanthus rupicola* J. Léonard, *Drypetes gossweileri*, *Spondianthus preussii* Engl. (Antidesmeae: Spondianthinae)], the Acalyphoideae [*Discoglypremna coloneura* Prain. (Carydendreae), *Mareya micrantha* (Benth.) Müll. Arg. (Acalypheae: Claoxylinae), *Trewia nudiflora*], and the Euphorbioideae (*Maprounea africana* Müll. Arg., *Sapium cornutum* Pax) (Hegnauer, 1989). These extremely bitter compounds also occur in the Cucurbitaceae, Brassicaceae (*Iberis*), Liliaceae (*Phormium*), Begoniaceae (*Begonia*), Rosaceae (*Purshia*), Datiscaceae, Sterculiaceae (*Helicteres*), Scrophulariaceae (*Gratiola*), Polemoniaceae (*Ipomopsis*), and Primulaceae (*Anagallis*).

MISCELLANEOUS COMPOUNDS

Amino acids. 3,4-Dihydroxy-L-phenylalanine (L-dopa) (**82**), a nonprotein amino acid, is used for treatment of Parkinson's disease. This compound is found in several plants, primarily legumes, but also occurs in *Euphorbia lathyrus* L. (Hegnauer, 1966b).

Coumarins. Many coumarins are essentially ubiquitous in higher plants. Compounds such as umbelliferone, esculin, esculetin, scopolin, scopoletin, and coumarin occur in many plant families. The bicoumarins euphorbetin and isoeuphorbetin are found in *Euphorbia lathyrus* (Euphorbioideae) (Rizk, 1987). Bergenin (**83**) derivatives are found in the bark of *Mallotus japonicus* Müll. Arg., *Mallotus repandus*, and *Macaranga peltata* Müll. Arg. (Acalyphoideae) and in *Flueggea microcarpa* Blume (Ramaiah et al., 1979; Rizk, 1987). Bergenin frequently accompanies ellagitannins in euphorbiaceous plants (Hegnauer, 1989). Benzocoumarins have been isolated from *Euphorbia royleana* Boiss. (Rizk, 1987).

Flavonoids. Flavonoids are ubiquitous components of plants. Several types, such as the glycosides of the flavones apigenin and luteolin, and the flavonols kaempferol and quercetin are found in a large percentage of plants examined. Other types of flavonoids, such as biflavonoids, are less widely distributed.

Numerous flavonoids have been isolated and characterized from members of the Euphorbiaceae (Rizk, 1987; Rizk & El-Missiry, 1986). Both *C*- and *O*-glycosides are found. Many compounds, such as quercetin and quercetin glycosides (e.g., isoquercitrin (**84**)), rutin, vitexin (**85**), isovitexin, isorhamnetin, orientin, isoorientin, kaempferol and kaempferol glycosides, rhamnetin, naringen gly-

cosides, apigenin and apigenin glycosides, quercitrin, isoquercitrin, and saponarin, as well as the anthocyanidins cyanidin, delphinidin, and pelargonidin are widespread within the Euphorbiaceae and also are found in many other plant families. Although the distribution of these glycosides might be useful for study of problems at lower hierarchical levels, most flavonoids are not particularly useful for study of relationships at higher taxonomic levels.

The presence of other, more unusual types of flavonoids has more promise in this regard. For example, 8-methoxyflavonoids [e.g., gossypetin (**86**)] are found in several taxa of the tribe Ricinocarpeae (subfamily Crotonoideae), including *Beyeria brevifolia* Baill., *B. leschenaultii*, *Ricinocarpos muricatus* Müll. Arg., and *R. stylosus* Diels (Rizk & El-Missiry, 1986).

Biflavonoids (e.g., heveaflavone (**87**)) are found in a number of families, including the Pinaceae, Anacardiaceae, Casuarinaceae, Clusiaceae, Ochnaceae, Rhamnaceae, Caprifoliaceae, and Euphorbiaceae (Geiger & Quinn, 1982). These compounds are also found in certain mosses, cycads, and in *Ginkgo biloba* L.

Hydrocarbons and waxy materials. Because many euphorbiaceous plants occur in deserts and dry areas, they have thick cuticles and a relatively large amount of waxy material (Gnecco et al., 1989; Rizk & El-Missiry, 1986). Most of the long chain hydrocarbons, alcohols, aldehydes, acids, and wax esters of the Euphorbiaceae are similar to those of other plant groups.

Candelilla wax of *Euphorbia antisyphilitica* Zucc., and the waxes of *E. cerifera* Alcocer, *Pedilanthus cymbiferus* Schltdl. (syn. *Pedilanthus aphyllus* Boiss.), and *Pedilanthus bracteatus* (Jacq.) Boiss. (syn. *Pedilanthus pavonis* Bois.) (Euphorbioideae: Euphorbieae: Euphorbiinae) are commonly used in cosmetics and as an extender in other wax products (Rizk, 1987; Schery, 1972). Candelilla wax is comprised of both hydrocarbon fractions and wax esters.

Monoterpenes. Monoterpenes are ubiquitous among plants. Few of the structures are so characteristic as to be useful in a chemosystematic sense with problems above the species level. Accumulation of monoterpenes as a class is common in the genus *Croton*, *Croton setigera* (*Eremocarpus setigerus*), and *Joannesia princeps* Vell. (Crotonoideae: Joannesieae) (Farnsworth et al., 1969; Hegnauer, 1966b, 1989). Few other taxa in the family accumulate significant quantities of these compounds in vegetative portions of the plant, although they are involved in attraction of pollinators in several taxa (e.g., *Dalechampia*).

Proteins and peptides. The seeds of several members of the Euphorbiaceae contain toxic proteins. For example, the castor bean, *Ricinus communis*, contains antigenic proteins that agglutinate defibrinated blood and red blood cells in vitro. As few as two to four seeds of this plant can be lethal, and eight are almost always lethal (Kingsbury, 1964). Ricin is a dimeric protein with two different peptide chains (MW 63,000). The seeds of *Aleurites fordii*, *Jatropha curcas* L., and *J. multifida* L. also produce toxic proteins that have not been studied extensively.

Rubber. Among the Euphorbiaceae, latex is found primarily in members of the subfamilies Crotonoideae and Euphorbioideae but generally is lacking in the Phyllanthoideae, Oldfieldioideae, and Acalyphoideae (Hegnauer, 1966b, 1989). Although latex is a complex mixture of diterpenes, triterpenes, enzymes, amino acids, and other components, polymeric isoprenoid compounds are important in most. Several plants of the Euphorbiaceae produce all *cis*-polyisoprene (natural rubber). Best known among these is *Hevea brasiliensis*, but similar materials are produced by other *Hevea* species, *Manihot glaziovii* Müll. Arg. (ceara or manicobe rubber), *Micrandra* species (Crotonoideae: Micrandreae: Micrandrinae) (caura rubber), and *Cnidoscolus* species (chilte rubber) (Rizk, 1987). Rubber has also been isolated from many *Euphorbia* species (Rizk, 1987).

Sesquiterpenes. Although several have been reported from the family, this class of compounds does not seem to be well represented (Ramaiah et al., 1979; Rizk, 1987).

Picrotoxins, a complex type of sesquiterpene, are found in the Menispermaceae (*Menispermum*, *Anamirta*, and *Cocculus*), the Coriariaceae, Orchidaceae (*Dendrobium*), and the Euphorbiaceae (*Hyaenanche*, Oldfieldioideae: Hyaenancheae) [e.g., pretoxin (**88**)] (Cane, 1981; Coscia, 1969). Mellitoxin is known to occur in *Hyaenanche globosa* Lamb. (Coscia, 1969).

Other compounds. A series of compounds including crotepoxide (**89**) is thought to be derived from *iso*-chorismic acid. This compound is found in *Croton macrostachys* Hochst. A series of α-glucosidase inhibitors, including α-homonojirimycin (**90**), has been described from *Omphalea diandra* L. (Euphorbioideae). These compounds resemble compounds found in legumes, the Moraceae, and the Polygonaceae and have promise as antitumor and antidiabetic drugs (Kite et al., 1988).

SYSTEMATIC VALUE OF CHEMICAL CHARACTERS

The chemistry of the Euphorbiaceae is among the most diverse of all plant families. As mentioned above, many of the most unusual classes of compounds are found only in this family and, hence, represent autapomorphic characters. Many others are of relatively simple biosynthetic origin and are widespread among higher plants.

Although the chemistry of most members of the family has been inadequately studied, our present knowledge of the chemistry of this family is becoming clearer and patterns are emerging. Undoubtedly, some surprises await additional phytochemical investigation.

Triterpenes are widespread in the Euphorbiaceae and are found in all five subfamilies. They are major components of the latex of the Crotonoideae and Euphorbioideae. Cucurbitacins (derived from triterpenes) are found in the Phyllanthoideae, Acalyphoideae, and Euphorbioideae.

Among the alkaloids, securinine alkaloids unite several genera of the Phyllanthoideae, and a series of nicotinic acid derived alkaloids, cyanogens, and 3-pyridones unite several genera of the Acalyphoideae.

The cyanogens of the Phyllanthoideae are all tyrosine derived, that of the Acalyphoideae nicotinic acid derived, and the cyanogens of the Crotonoideae are valine/isoleucine derived.

Kaurene derived diterpenes are found in the Crotonoideae and Oldfieldioideae. Monocyclic derived diterpenes are found in the Acalyphoideae, Crotonoideae, and Euphorbioideae. Cocarcinogenic diterpenes derived from these precursors are found commonly in the Euphorbioideae and Crotonoideae. Highly oxygenated diterpenes based on a labdane skeleton are found in the Crotonoideae and Acalyphoideae.

In summary, several chemical features serve to link the five subfamilies. The Oldfieldioideae have been insufficiently studied.

There are few chemical similarities between the Flacourtiaceae and the Euphorbiaceae (Hegnauer, 1989).

Many species of the genera *Buxus*, *Pachysandra*, and *Sarcococca* possess unusual steroidal and triterpenoid alkaloids. These compounds are found only in the Buxaceae and are distinct from those of euphorbiaceous plants (some are similar to the alkaloids of plants in the Apocynaceae). A number of relatively common triterpenes found in the genus *Buxus* also occur in the Euphorbiaceae (Hegnauer, 1989). Although *Simmondsia* is sometimes considered to be a member of the Euphorbiaceae, these plants lack the alkaloids characteristic of the Buxaceae and Euphorbiaceae and have unusual nitriles not found in either family (Hegnauer, 1989).

The triterpene alkaloids of the Daphniphyllaceae are unique and do not resemble those of the Euphorbiaceae (Hegnauer, 1989; Rizk, 1987). There is no significant chemical similarity between this family and the Euphorbiaceae.

The Celastraceae and Rhamnaceae both have peptide and maytansanoid alkaloids similar to those of several genera of Euphorbiaceae (Hegnauer, 1989). Benzylisoquinoline alkaloids also are known from the Rhamnaceae (*Rhamnus*, *Phylica*, *Colletia*, *Colubrina*, *Discaria*, *Ratanilla*, *Talguenea*, and *Zizyphus*) as well as from the Euphorbiaceae (primarily the genus *Croton*). Many relatively common types of triterpenes are found in these families along with certain oxidatively altered ones. The spectrum of other compounds in the Celastraceae and Rhamnaceae (including sesquiterpene and spermine alkaloids, anthraquinone and naphthaquinone pigments, seed lipids, and cardiac glycosides) is not particularly similar to those of euphorbiaceous plants.

Some unusual lipids occur in seeds of the Malvaceae, Sterculiaceae, and Bombacaceae; cyclopropenoid fatty acids are especially common (Hegnauer, 1989; Smith, 1970). Peptide alkaloids are found in the Sterculiaceae (*Melochia* and *Waltheria*) as well as in euphorbiaceous genera. Overall, the chemistry of plants typically placed in the Malvales (Malvaceae, Sterculiaceae, Bombacaceae, Tiliaceae, Elaeocarpaceae, etc.) shows some similarity, but does not strongly resemble that of the Euphorbiaceae.

The chemistry of members of the Geraniales (Geraniaceae, Oxalidaceae, Limnanthaceae, Tropaeolaceae, Balsaminaceae, Linaceae, Erythroxylaceae, Humiriaceae, Zygophyllaceae, Malpighiaceae, Trigoniaceae, Polygalaceae, Krameriaceae, Vochysiaceae, etc.) does not greatly resemble that of the Euphorbiaceae. The Limnanthaceae and Tropaeolaceae contain glucosinolates, as does the euphorbiaceous genus *Drypetes* (and *Putranjiva*, if not included in *Drypetes*). Several species of the genus *Linum* are cyanogenic and contain the cyanogenic compounds linamarin, lotaustralin, linustatin, and neolinustatin, as do some members of the Crotonoideae. However, linamarin and lotaustralin are the most widespread of all cyanogenic compounds among higher plants. Many species of the Geraniaceae accumulate monoterpenes. The floral lipids of the Malpighiaceae and Krameriaceae contain unusual fatty acid and glyceride mixtures, but these are not found in the Euphorbiaceae (al-

though equally unusual floral lipids are found in species of *Dalechampia*). The tropane alkaloids of coca are found in *Erythroxylum* (Erythroxylaceae), and also in other families, especially the Solanaceae (Seigler, 1977).

The Thymelaeaceae have the strongest chemical link to the Euphorbiaceae. Because of the complex and lengthy biosynthetic pathways leading to the formation of cocarcinogenic diterpenes and their highly restricted distribution (only in the Euphorbiaceae and Thymelaeaceae), it seems highly probable that the families are closely related. This relationship has been observed on a basis of more classical characters as well; both Dahlgren et al. (1981) and Thorne (1981) placed the Euphorbiaceae and Thymelaeaceae close together in their respective phylogenetic systems. Other strong chemical similarities between the two families are not yet fully understood; the chemistry of plants of the Thymelaeaceae has not been thoroughly studied.

Perhaps the chemical data speak best for the situation described by Webster (1987), in which the Euphorbiaceae are derived from some group intermediate to the Geraniales and Malvales. It seems likely that the chasm between the Dilleniidae and Rosidae (Cronquist, 1981) has been exaggerated. The Thymelaeaceae probably are closely related to the Euphorbiaceae, although, perhaps, they should be placed in a parallel but distinct order. Other affinities are suggested with the Rhamnaceae and Celastraceae.

Although chemical data are helpful in understanding the affinities of this most enigmatic family, the final resolution of the phylogenetic placement of the Euphorbiaceae remains a goal to be determined through future research based on a combination of molecular, phytochemical and morphological approaches.

Literature Cited

Adolf, W., E. H. Seip & E. Hecker. 1988. Irritant principles of the mezereon family (Thymelaeaceae). V. New skin irritants and tumor promoters of the daphnane and 1α-alkyldaphnane type from *Synaptolepis kirkii* and *Synaptolepis retusa*. J. Nat. Prod. (Lloydia) 51: 662–674.

Adsersen, A., H. Adsersen & L. Brimer. 1987. Cyanogenic constituents in plants from the Galápagos Islands. Biochem. Syst. & Ecol. 16: 65–77.

Bagavathi, R., B. Sorg & E. Hecker. 1988. Tigliane-type diterpene esters from *Synadenium grantii*. Pl. Med. 506–510.

Bajaj, R., C. J. Chang, J. L. McLaughlin, R. G. Powell & C. R. Smith, Jr. 1986. Tiliroside from the seeds of *Eremocarpus setigerus*. J. Nat. Prod. (Lloydia) 49: 1174–1175.

Bakker, H. J., E. L. Ghisalberti & P. R. Jefferies. 1972. Biosynthesis of diterpenes in *Beyeria leschenaultii*. Phytochemistry 11: 2221–2231.

Beutler, J. A. & A. N. Brubaker. 1987. The chemistry and pharmacology of the securinine alkaloids. Drugs of the Future 12: 957–976.

———, A. B. Alvarado, T. G. McCloud & G. M. Cragg. 1989. Distribution of phorbol ester activity in the Euphorbiaceae. Phytotherapy Research 3: 188–192.

Bharucha, K. E. & F. D. Gunstone. 1956. Vegetable oils. V. Component acids of *Cephalocroton cordofanus* seed oil. J. Sci. Food Agric. 7: 606–609.

Bisset, N. S. 1985. Plants as a source of isoquinoline alkaloids. Pp. 1–2 *in* J. D. Phillipson, M. F. Roberts & M. H. Zenk (editors), The Chemistry and Biology of Isoquinoline Alkaloids. Springer-Verlag, Berlin.

Burke, B. A., W. R. Chan, E. C. Prince, P. S. Manchand, N. Eickman & J. Clardy. 1976. The structure of corylifuran, a clerodane-type diterpene from *Croton corylifolius* Lam. Tetrahedron 32: 1881–1884.

Calderwood, R. C. & F. C. Gunstone. 1953. Structure of kamolenic acid. Chem. Industry 436–437.

Cane, D. E. 1981. Biosynthesis of sesquiterpenes. Pp. 283–374 *in* J. W. Porter & S. L. Spurgeon (editors), Biosynthesis of Isoprenoid Compounds, Vol. 1. Wiley, New York.

Coscia, C. J. 1969. Picrotoxin. Pp. 147–202 *in* W. I. Taylor & A. R. Battersby (editors), Cyclopentanoid Terpene Derivatives. Dekker, New York.

Cronquist, A. 1981. An Integrated System of Classification of Flowering Plants. Columbia Univ. Press, New York.

Croteau, R. & M. A. Johnson. 1985. Biosynthesis of terpenoid wood extractives. Pp. 349–439 *in* T. Higuchi (editor), Biosynthesis and Biodegradation of Wood Components. Academic Press, Orlando.

Dahlgren, R. M. T., S. R. Jensen & B. J. Nielsen. 1981. A revised classification of the angiosperms with comments on correlation between chemical and other characters. Pp. 149–204 *in* D. A. Young & D. S. Seigler (editors), Phytochemistry and Angiosperm Phylogeny. Praeger, New York.

Das, M. C. & S. B. Mahato. 1983. Triterpenoids. Phytochemistry 22: 1071–1095.

Dell, B. & A. J. McComb. 1974. Resin production and glandular hairs in *Beyeria viscosa* (Labill.) Miq. (Euphorbiaceae). Austral. J. Bot. 25: 195–210.

Evans, F. J. 1986a. Macrocyclic diterpenes of the family Euphorbiaceae. Pp. 139–170 *in* F. J. Evans (editor), Naturally Occurring Phorbol Esters. CRC Press, Boca Raton, Florida.

———. 1986b. Phorbol: Its esters and derivatives. Pp. 171 216 *in* F. J. Evans (editor), Naturally Occurring Phorbol Esters. CRC Press, Boca Raton, Florida.

——— & A. D. Kinghorn. 1977. A comparative phytochemical study of the diterpenes of some species of the genera *Euphorbia* and *Elaeophorbia* (Euphorbiaceae). Bot. J. Linn. Soc. 74: 23–35.

——— & R. J. Schmidt. 1980. Plants and plant products that induce contact dermatitis. Pl. Med. 38: 289–316.

——— & C. J. Soper. 1978. The tigliane, daphnane and ingenane diterpenes, their chemistry, distribution, and biological activities. A review. J. Nat. Prod. (Lloydia) 41: 193–233.

FARNSWORTH, N. R., R. N. BLOMSTER, W. M. MESMER, J. C. KING, G. J. PERSINOS & J. D. WILKES. 1969. A phytochemical and biological review of the genus *Croton*. J. Nat. Prod. (Lloydia) 32: 1 28.

FODOR, G. B. & B. COLOSANTI. 1985. The pyridine and piperidine alkaloids: Chemistry and pharmacology. Pp. 1–90 *in* S. W. Pelletier (editor), Alkaloids: Chemical and Biological Perspectives, Vol. 3. Wiley, New York.

GEIGER, H. & C. QUINN. 1982. Biflavonoids. Pp. 505–534 *in* J. B. Harborne & T. J. Mabry (editors), The Flavonoids: Advances in Research. Chapman and Hall, London.

GHISALBERTI, E. L., P. R. JEFFRIES & M. A. SEFTON. 1978. Secobeyerane. Diterpenes from *Beyeria calycina*. Phytochemistry 17: 1961–1965.

GNECCO, S., J. BARTULIN, J. BECERRA & C. MARTICORENA. 1989. *n*-Alkanes from Chilean Euphorbiaceae and Compositae species. Phytochemistry 28: 1254–1256.

HASMA, H. & A. SUBRAMANIAM. 1978. The occurrence of a furanoid fatty acid in *Hevea brasiliensis* latex. Lipids 13: 905–907.

HECKER, E. 1977. New toxic, irritant and cocarcinogenic diterpene esters from Euphorbiaceae and Thymelaeaceae. Pure Appl. Chem. 49: 1423–1431.

———. 1986. Tumour promoters of the irritant diterpene ester type as risk factors of cancer in man. Bot. J. Linn. Soc. 94: 197–219.

——— & R. SCHMIDT. 1974. Phorbolesters—The irritants and cocarcinogens of *Croton tiglium*. Fortschr. Chem. Organischer Naturst. 31: 378–467.

HEGNAUER, R. 1963. The taxonomic significance of alkaloids. Pp. 389–427 *in* T. Swain (editor), Chemical Plant Taxonomy. Academic Press, London.

———. 1966a. Comparative phytochemistry of alkaloids. Pp. 211–230 *in* T. Swain (editor), Comparative phytochemistry. Academic Press, London.

———. 1966b. Euphorbiaceae. Pp. 103–140 *in* Chemotaxonomie der Pflanzen, Vol. 4. Birkhäuser Verlag, Basel.

———. 1989. Euphorbiaceae. Pp. 440–474 *in* Chemotaxonomie der Pflanzen, Vol. 8. Birkhäuser Verlag, Basel.

HEIMERMANN, W. H. & R. T. HOLMAN. 1972. Highly optically active triglycerides of *Sebastiana ligustrina*. Phytochemistry 11: 799–802.

HOWARD, A. S. & J. P. MICHAEL. 1986. Simple indolizidine and quinolizidine alkaloids. Pp. 183–308 *in* A. Brossi (editor), The Alkaloids, Vol. 28. Academic Press, New York.

HURUSAWA, I. 1954. Eine nochmalige Durchsicht des herkommlichen Systems der Euphorbiaceen im weiteren Sinne. J. Fac. Sci. Univ. Tokyo 6: 209–342.

JACOBSON, M., M. M. CRYSTAL & J. D. WARTHEN, JR. 1981. Boll weevil feeding deterrents from tung oil. J. Agric. Food Chem. 29: 591–593.

JOHNS, S. R. & J. A. LAMBERTON. 1967. New imidazole alkaloids from a *Glochidion* species (Family Euphorbiaceae). Austral. J. Chem. 20: 555–560.

———, ——— & A. A. SIOUMIS. 1970. N_a-methyltetrahydroharman from *Spathiostemon javensis*. Austral. J. Chem. 23: 213.

JOLAD, S. D., J. J. HOFFMANN, K. H. SCHRAM, J. R. COLE, M. S. TEMPESTA & R. B. BATES. 1982. Constituents of *Eremocarpus setigerus*. J. Organic Chem. 47: 1356–1358.

KAWASHIMA, T., T. NAKATSU, Y. FUKAZAWA & S. ITO. 1976. Diterpenic lactones of *Mallotus repandus*. Heterocycles 5: 227–232.

KHAN, M. I., M. IKRAM & S. F. HUSSAIN. 1983. Bisbenzylisoquinoline alkaloids from *Andrachne cordifolia*. Pl. Med. 47: 191.

KINGHORN, A. D. 1979. Cocarcinogenic irritant Euphorbiaceae. Pp. 137–159 *in* A. D. Kinghorn (editor), Toxic Plants. Columbia Univ. Press, New York.

KINGSBURY, J. M. 1964. Poisonous Plants of the U.S. and Canada. Prentice Hall, Englewood Cliffs, New Jersey.

KITE, G. C., L. E. FELLOWS, G. W. J. FLEET, P. S. LIU, A. M. SCOFIELD & N. G. SMITH. 1988. α-Homonojirimycin [2,6-dideoxy-2,6-imino-D-glycero-L-gulohepitol] from *Omphalea diandra* L.: Isolation and glucosidase inhibition. Tet. Let. 29: 6483–6486.

KLEIMAN, R., R. D. PLATTNER & G. F. SPENCER. 1977. *Alchornea cordifolia* seed oil: A rich source of a new C_{20} epoxide, (+)-*cis*-14,15-epoxy-*cis*-11-eicosenoic acid. Lipids 12: 610–612.

———, C. R. SMITH, JR., S. G. YATES & Q. JONES. 1965. Search for new industrial oils. XII. Fifty-eight Euphorbiaceae oils, including one rich in vernolic acid. J. Amer. Oil Chem. Soc. 42: 169–172.

LAUTER, W. M. & P. A. FOOTE. 1955. Toxic principles of *Hippomane mancinella* II. Isolation of a toxic principle. J. Amer. Pharm. Assoc. 44: 361–363.

LIEBEREI, R. 1986. Cyanogenesis during infection of *Hevea brasiliensis* with *Microcyclus ulei*. J. Phytopathol. 115: 134–146.

———. 1988. Relationship of cyanogenic capacity (HCN-c) of the rubber tree *Hevea brasiliensis* to susceptibility to *Microcyclus ulei*, the agent causing South American leaf blight. J. Phytopathol. 122: 54–67.

———, D. SELMAR & B. BIEHL. 1985. Metabolization of cyanogenic glycosides in *Hevea brasiliensis*. Plant Syst. Evol. 150: 49–63.

MAAT, L. & H. C. BEYERMAN. 1983. The imidazole alkaloids. *In* A. Brossi (editor), The Alkaloids, Vol. 22. Academic Press, New York.

MAHLBERG, P. G., J. PLESZCZYNSKA & M. FURR. 1988. Latex triterpenoid profiles of normal and cristata taxa of *Euphorbia* and their application as chemotaxonomic characters. Monogr. Syst. Bot. Missouri Bot. Gard. 25: 623–629.

MANNERS, G. D. 1987. The role of phytochemistry in attacking the leafy spurge (*Euphorbia esula*). Pp. 228–237 *in* G. R. Waller (editor), Allelochemicals: Role in Agriculture and Forestry (A.C.S. Symposium, Vol. 330). American Chemical Society, Washington, D.C.

MCGARRY, E. J., K. H. PEGEL, L. PHILLIPS & E. S. WAIGHT. 1971. The constitution of the aromatic diterpene cleistanthol. J. Chem. Soc., Sec. C, 904–909.

NAHRSTEDT, A. 1982. Strukturelle Beziehungen zwischen pflanzlichen und tierischen Sekundärstoffe. Pl. Med. 44: 2–14.

———. 1987. Recent developments in chemistry, distribution, and biology of the cyanogenic glycosides. Pp. 213–234 *in* K. Hostettmann & P. J. Lea (editors), Biologically Active Natural Products. Clarendon Press, Oxford.

OKUDA, T., K. MORI & T. HATANO. 1980. The distri-

bution of geraniin and mallotusinic acid in the order Geraniales. Phytochemistry 19: 547–551.

———, T. Yoshida, N. Shiola & J. Nobuhara. 1975. A new amino acid from seeds of *Aleurites fordii*. Phytochemistry 14: 2304–2305.

Ourisson, G., M. Rohmer & R. Anton. 1979. Macroevolution and microevolution. Pp. 131–162 *in* T. Swain & G. R. Waller (editors), Topics in the Biochemistry of Natural Products (Rec. Adv. Phytochem., Vol. 13). Plenum, New York.

Pais, M., J. Marchand, X. Monseur, F. Jarreau & R. Goutarel. 1967. Chemie organique.—Alcaloïdes peptidiques. Structure de l'hymenocardine, alcaloïde de l'*Hymenocardia acida* Tul. (Euphorbiacées). Compt. Rend. Hebd. Séances Acad. Sci. 264: 1409–1411.

Pant, P. & R. P. Rastogi. 1979. The triterpenoids. Phytochemistry 18: 1095–1108.

Pegel, K. H., L. P. L. Piacenza, L. Phillips & E. S. Waight. 1971. *ent*-3β-Hydroxybeyer-15(16)-ene-2,12-dione from *Androstachys johnsonii* Prain. (Euphorbiaceae). Chem. Communications 1346 1347.

Ponsinet, G. & G. Ourisson. 1965. Etudes chimiotaxonomiques dans la famille des euphorbiacées—I. Introduction générale et separation et identification des triterpènes tetracycliques monohydroxylés naturels. Phytochemistry 4: 799–811.

———, G. Ourisson & A. C. Oehlschlager. 1968. Systematic aspects of the distribution of di- and triterpenes. Pp. 271–302 *in* T. J. Mabry, R. E. Alston & V. C. Runeckles (editors), Recent Advances Phytochem., Vol. 1. Appleton-Century-Crofts, New York.

Powell, R. G., D. Weisleder & C. R. Smith, Jr. 1981. Novel maytansinoid tumor inhibitors from *Trewia nudiflora*: Trewiasine, dehydrotrewiasine, and demethyltrewiasine. J. Organic Chem. 46: 4398-4403.

———, ——— & ———. 1985. Daphnane diterpenes from *Diarthron vesiculosum*: Vesiculosin and isovesiculosin. J. Nat. Prod. (Lloydia) 48: 102–107.

———, C. R. Smith, Jr., R. D. Plattner & B. E. Jones. 1983. Additional new maytansinoids from *Trewia nudiflora*: 10-epitrewiasine and nortrewiasine. J. Nat. Prod. (Lloydia) 46: 660–666.

Radcliffe-Smith, A. 1986. A review of the family Euphorbiaceae. Pp. 63–85 *in* F. J. Evans (editor), Naturally Occurring Phorbol Esters. CRC Press, Boca Raton, Florida.

Ramaiah, P. A., L. R. Row, D. S. Reddy, A. S. R. Anjaneyulu, R. S. Ward & A. Pelter. 1979. Isolation and characterization of bergenin derivatives from *Macaranga peltata*. J. Chem. Soc., Perkin Trans. I, 2313–2316.

Reider, P. J. & D. M. Roland. 1984. Maytansinoids. Pp. 71 156 *in* A. Brossi (editor), The Alkaloids, Vol. 23. Academic Press, New York.

Rizk, A. M. 1987. The chemical constituents and economic plants of the Euphorbiaceae. Bot. J. Linn. Soc. 94: 293–326.

——— & M. M. El-Missiry. 1986. Non diterpenoid constituents of Euphorbiaceae and Thymelaeaceae. Pp. 107 138 *in* F. J. Evans (editor), Naturally Occurring Phorbol Esters. CRC Press, Boca Raton, Florida.

Roberts, K. D., E. Weiss & T. Reichstein. 1966. Die Cardenolide der Samen von *Mallotus paniculatus* Muell. Arg. (Euphorbiaceae). Helv. Chim. Acta 49: 316–329.

Rodman, J. E. 1991a. A taxonomic analysis of glucosinolate-producing plants, part 1: Phenetics. Syst. Bot. 16: 598–618.

———. 1991b. A taxonomic analysis of glucosinolate-producing plants, part 2: Cladistics. Syst. Bot. 16: 619–629.

———, R. A. Price, K. Karol, E. Conti, K. J. Sytsma & J. D. Palmer. 1993. Nucleotide sequences of the *rbc*L gene indicate monophyly of mustard oil plants. Ann. Missouri Bot. Gard. 80: 686 699.

Sastry, S. D. & G. R. Waller. 1972. Biosynthesis of *N*-methyl-5-carboxamid-2-pyridone from *Trewia nudiflora*. Phytochemistry 11: 2241–2245.

Sato, A., A. Ogiso & H. Kuwano. 1980. Acyclic diterpenes from *Croton kerrii*. Phytochemistry 19: 2207–2209.

Schery, R. W. 1972. Plants for Man, 2nd Ed. Prentice Hall, Englewood Cliffs, New Jersey.

Schmidt, R. J. 1986a. The daphnane polyol esters. Pp. 217–244 *in* F. J. Evans (editor), Naturally Occurring Phorbol Esters. CRC Press, Boca Raton, Florida.

———. 1986b. The ingenane polyol esters. Pp. 245-270 *in* F. J. Evans (editor), Naturally Occurring Phorbol Esters. CRC Press, Boca Raton, Florida.

———. 1986c. Biosynthetic and chemosystematic aspects of the Euphorbiaceae and Thymelaeaceae. Pp. 87–106 *in* F. J. Evans (editor), Naturally Occurring Phorbol Esters. CRC Press, Boca Raton, Florida.

———. 1987. The biosynthesis of tigliane and related diterpenoids; an intriguing problem. Bot. J. Linn. Soc. 94: 221–230.

Schmidt, U., A. Lieberknecht & E. Haslinger. 1985. Peptide alkaloids. Pp. 299–326 *in* A. Brossi (editor), The Alkaloids, Vol. 26. Academic Press, New York.

Seigler, D. S. 1977. Plant systematics and alkaloids. Pp. 1–82 *in* R. H. F. Manske (editor), The Alkaloids, Vol. 16. Academic Press, New York.

———. 1981a. Terpenes and plant phylogeny. Pp. 117–148 *in* D. A. Young & D. S. Seigler (editors), Phytochemistry and Angiosperm Phylogeny. Praeger, New York.

———. 1981b. Secondary metabolites and plant systematics. Pp. 139–176 *in* E. E. Conn (editor), The biochemistry of Plants, Vol. 7. Secondary Plant Products. Academic Press, New York.

Smith, C. R., Jr. 1970. Occurrence of unusual fatty acids in plants. Prog. Chem. Fats Other Lipids 11: 139–177.

Strunz, G. M. & J. A. Findlay. 1985. Pyridine and piperidine alkaloids. Pp. 89–183 *in* A. Brossi (editor), The Alkaloids, Vol. 26. Academic Press, New York.

Thorne, R. F. 1981. Phytochemistry and angiosperm phylogeny. A summary statement. Pp. 233–295 *in* D. A. Young & D. S. Seigler (editors), Phytochemistry and Angiosperm Phylogeny. Praeger, New York

Valen, F. van. 1978. Contribution to the knowledge of cyanogenesis in Angiosperms, 10. Communicaton. Cyanogenesis in Euphorbiaceae. Pl. Med. 34: 408–413.

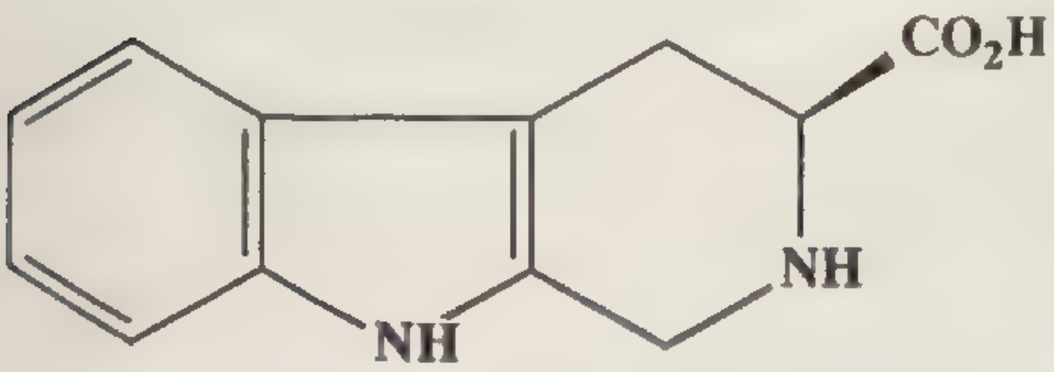
Waller, G. R. & E. K. Nowacki. 1978. Alkaloid Biology and Metabolism in Plants. Plenum, New York.

Webster, G. L. 1975. Conspectus of a new classification of the Euphorbiaceae. Taxon 24: 593 601

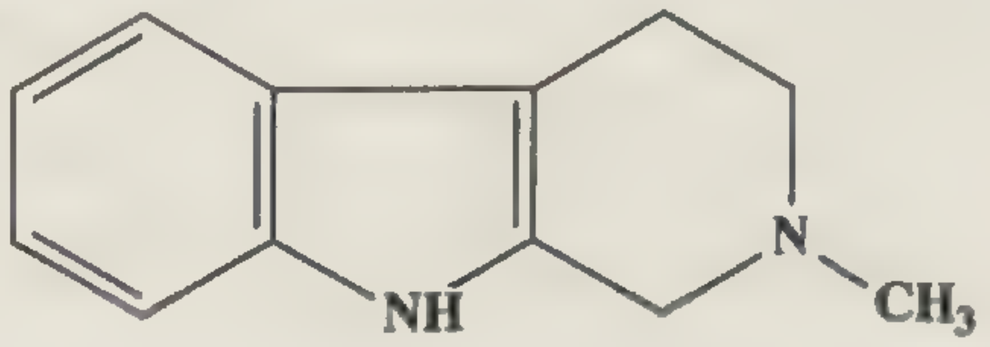
———. 1987. The saga of the spurges: A review of classification and relationships in the Euphorbiales. Bot. J. Linn. Soc. 94: 3–46.

———. 1992. Realignments in American *Croton* (Euphorbiaceae). Novon 2: 269–273.

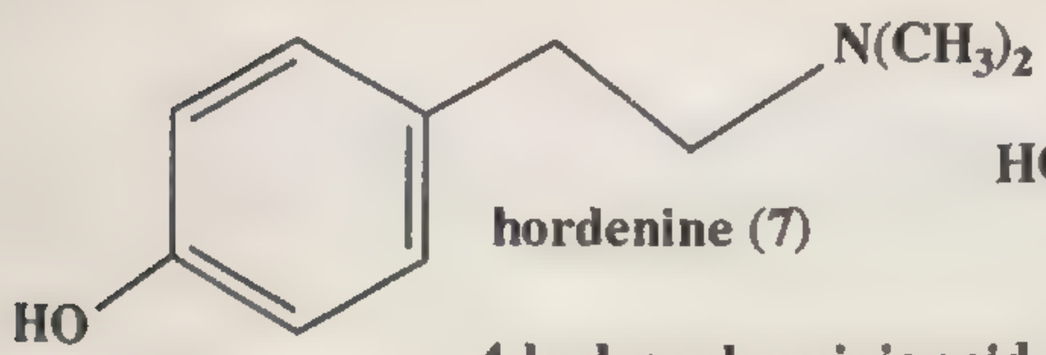
———. 1994. Synopsis of the genera and suprageneric taxa of Euphorbiaceae. Ann. Missouri Bot. Gard. 81: 33–144.



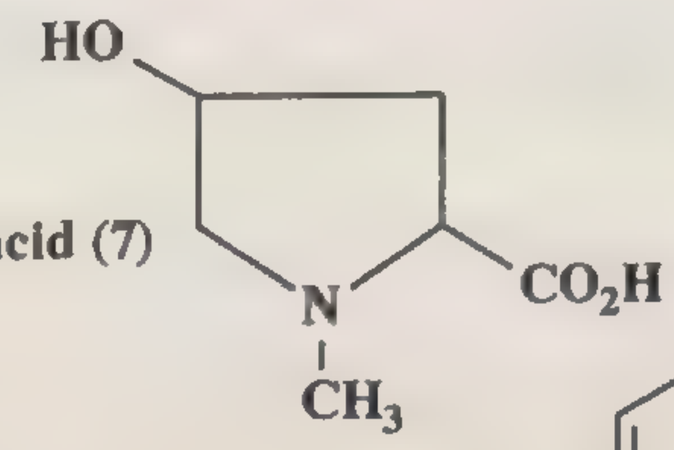
L-3-carboxy-1,2,3,4-tetrahydrocarboline (1)



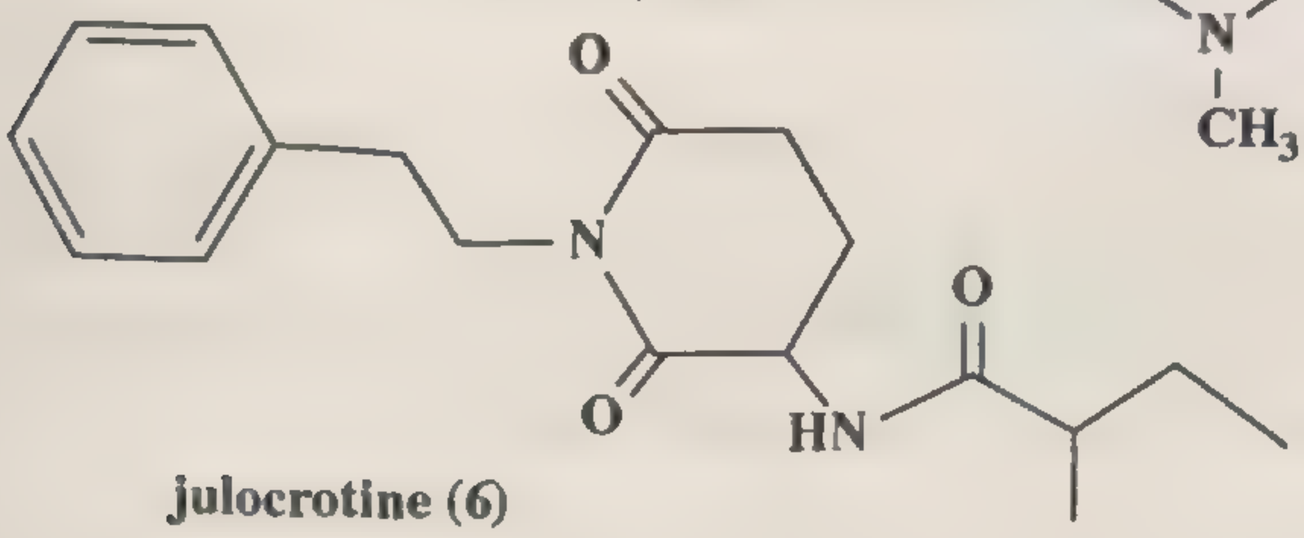
Nβ-methyltetrahydroharman (2)



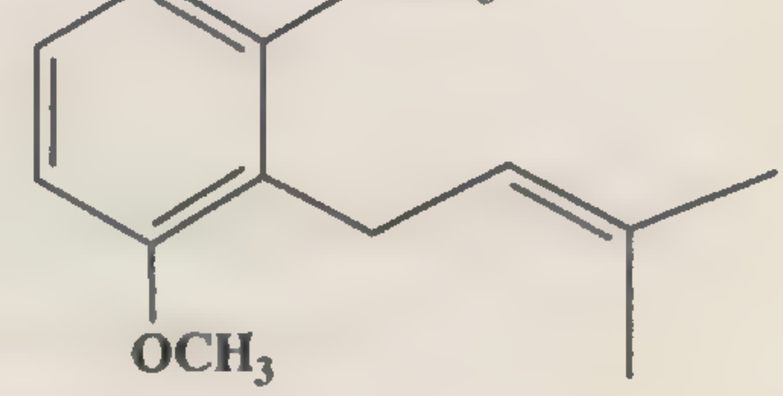
hordenine (7)



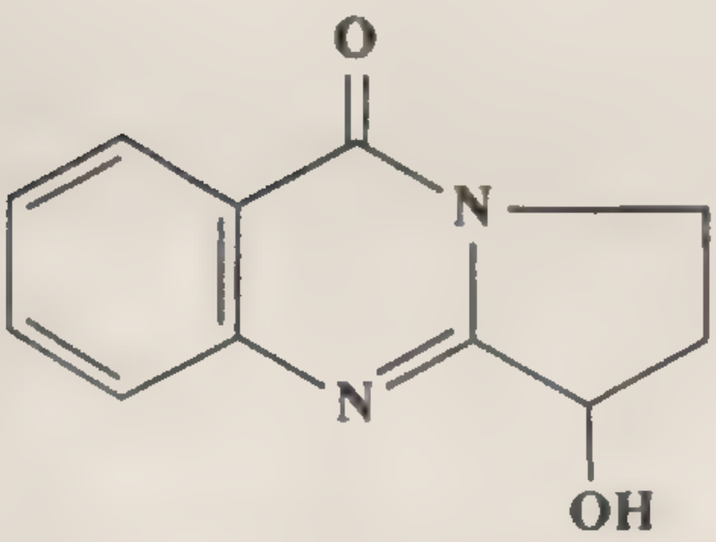
4-hydroxyhygrinic acid (7)



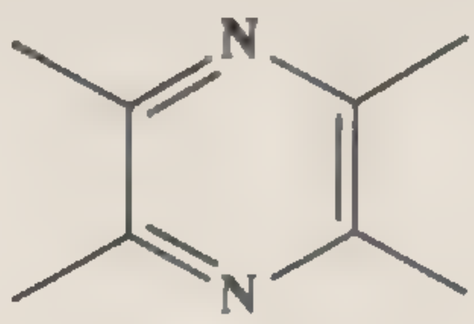
julocrotine (6)



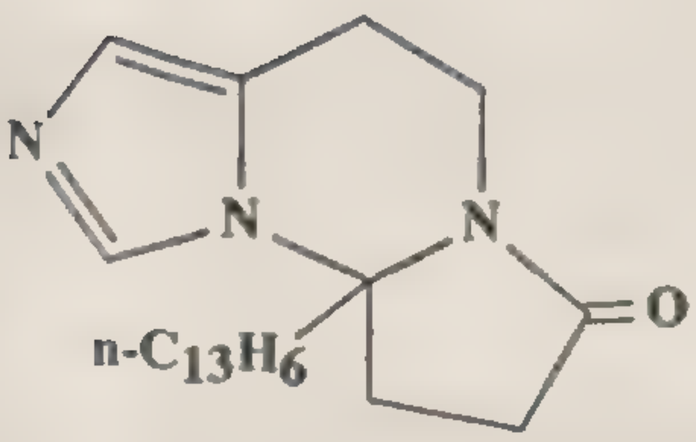
2,4-dimethoxy-Ψ,Ψ-dimethyl-allyl-*E*-cinnamoylpiperidide (5)



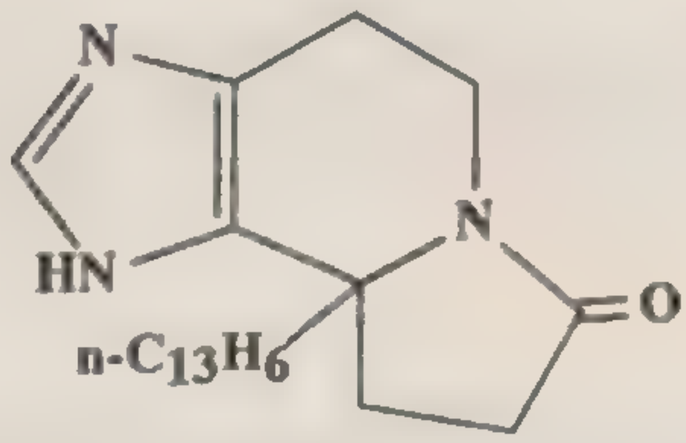
vasicine (3)



tetramethylpyrazine (9)

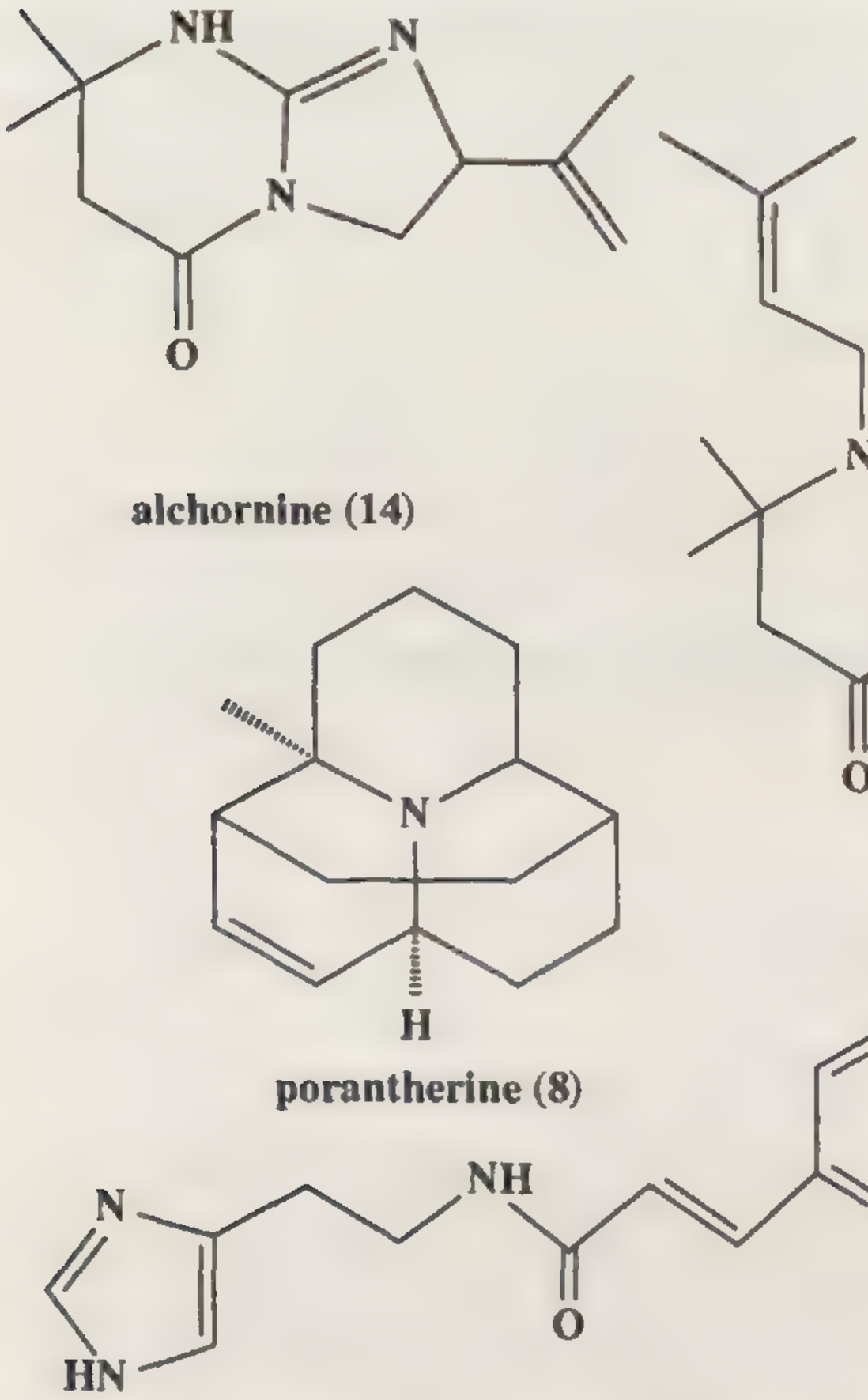


glochidine (12)



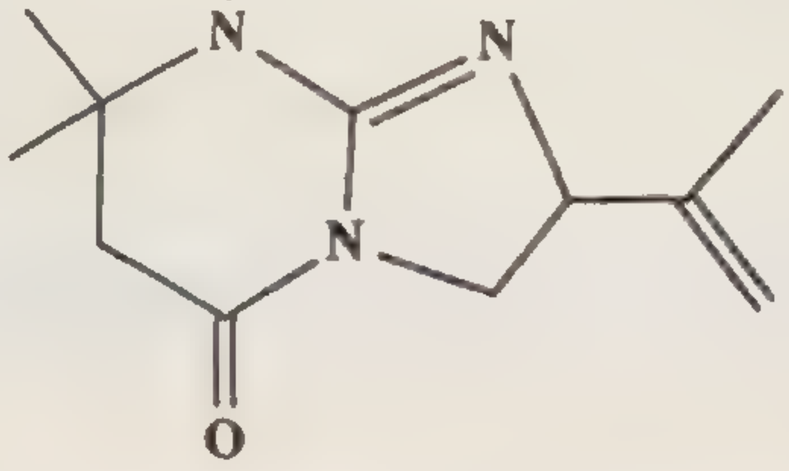
glochidicine (11)

FIGURE. Chemical structures found in Euphorbiaceae grouped by chemical type. The number of each structure corresponds to the boldface number in parentheses following the chemical name in the text. Compounds number 1–29 and 31–32 are alkaloids, 30 and 33–37 are cyanogenic glycosides, 38–52 are diterpenes, 53–54 are glucosinolates, 55–67 are fatty acids, 68–70 are hydrolyzable tannins, 71–81 are triterpenes, 82 is an amine, 83 is a coumarin, 84–87 are flavonoids, 88 is a sesquiterpene, 89 are of other biosynthetic origin.



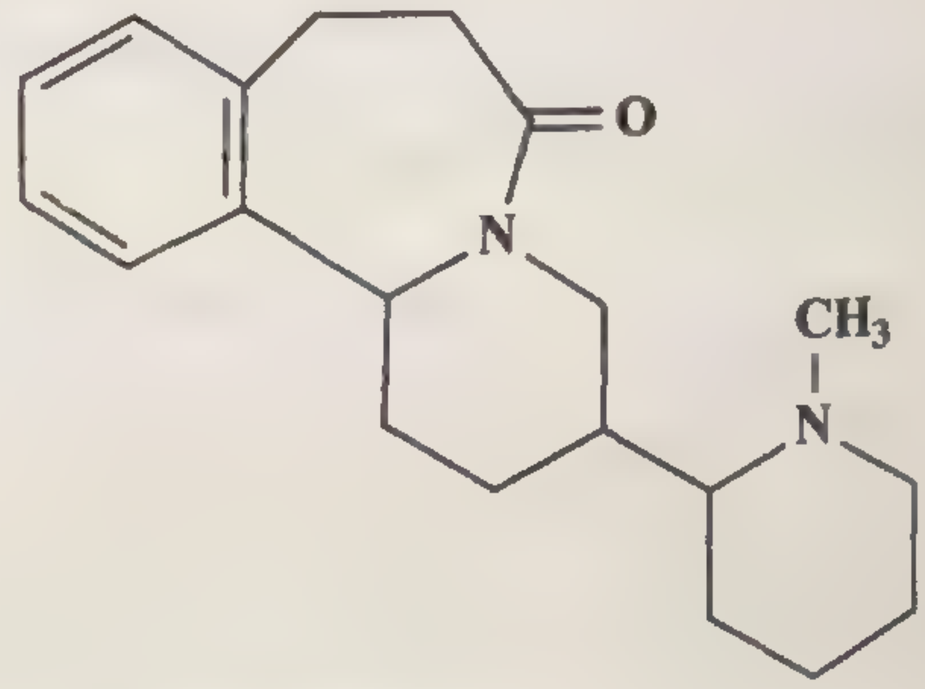
alchornine (14)

Nα-oxodecanoylhistamine (10)

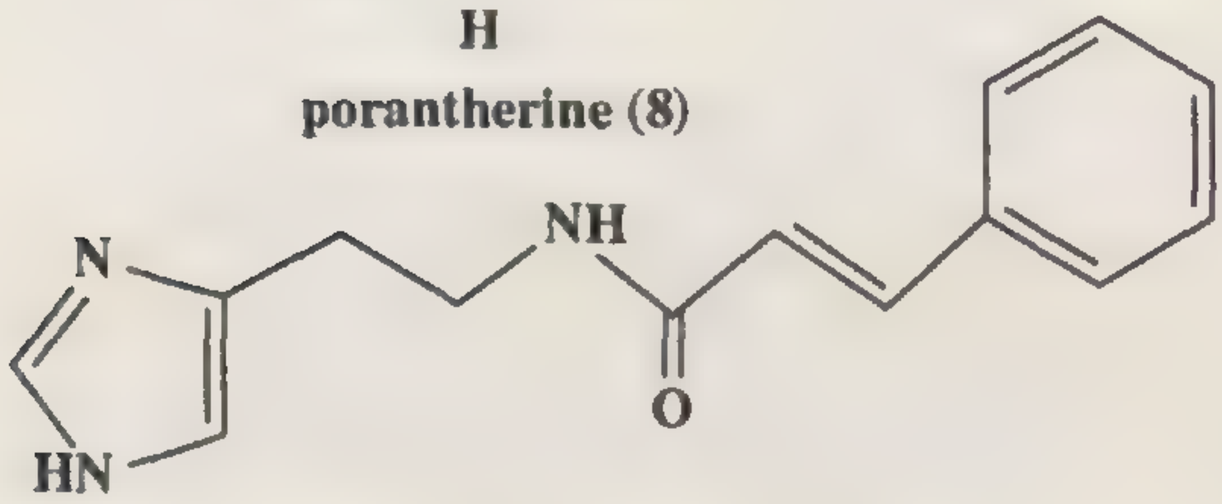


alchornidine (13)

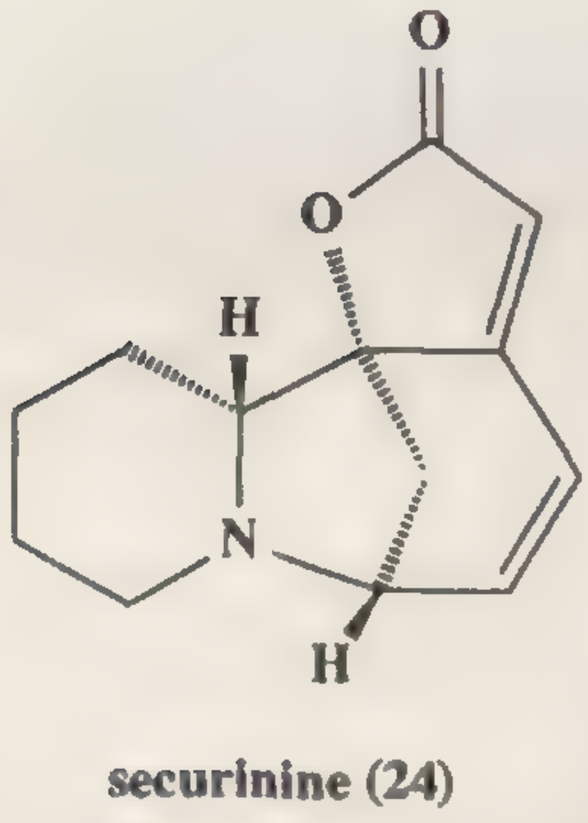
porantherine (8)



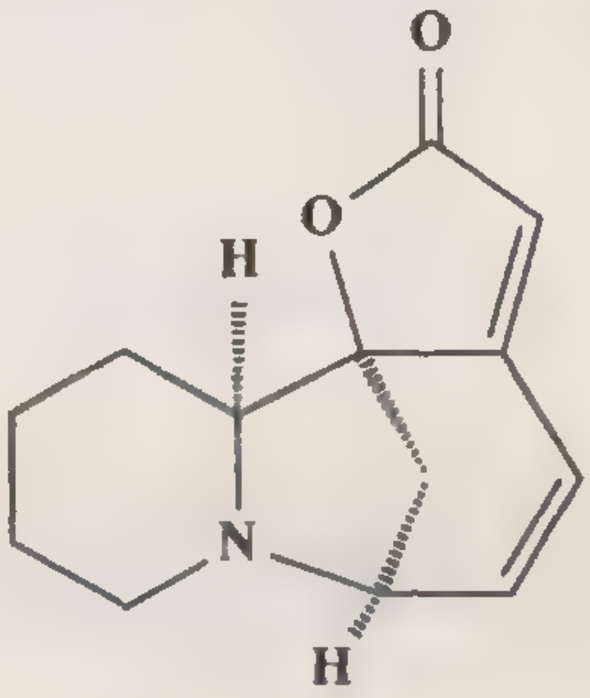
astrocasine (4)



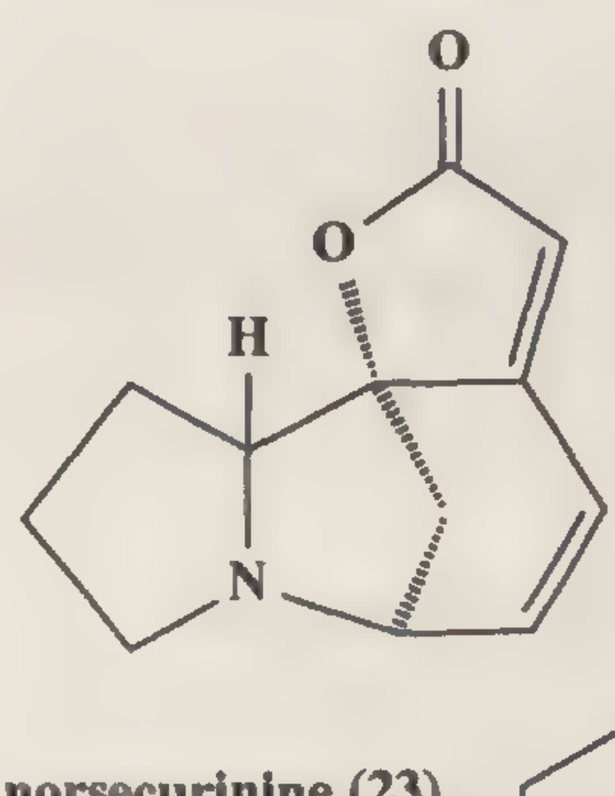
Nα-cinnamoylhistamine (15)



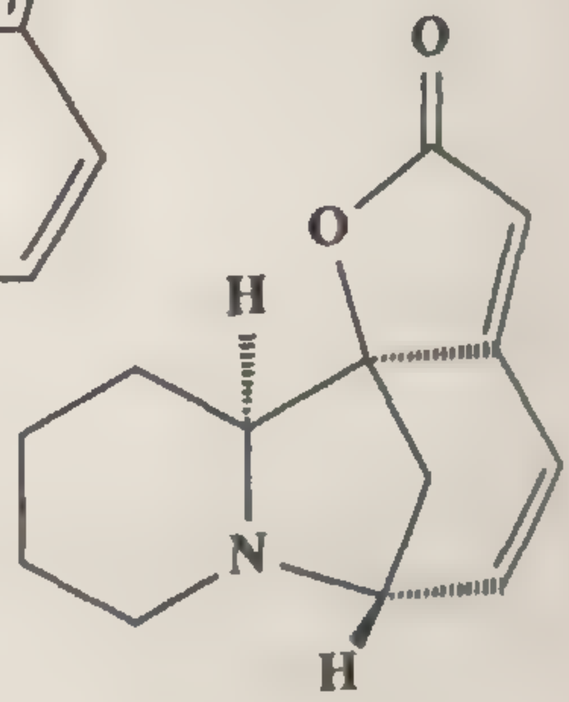
securinine (24)



allosecurinine (22)

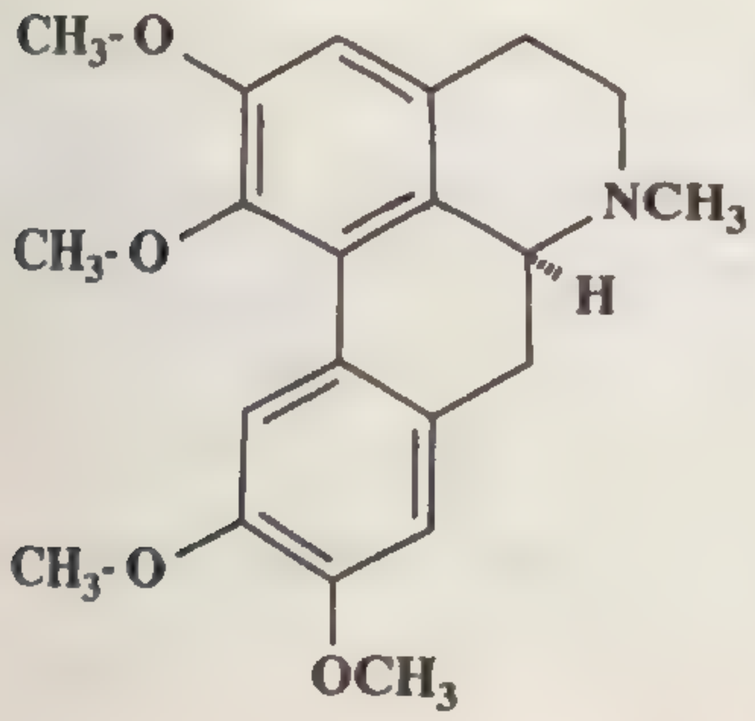


norsecurinine (23)

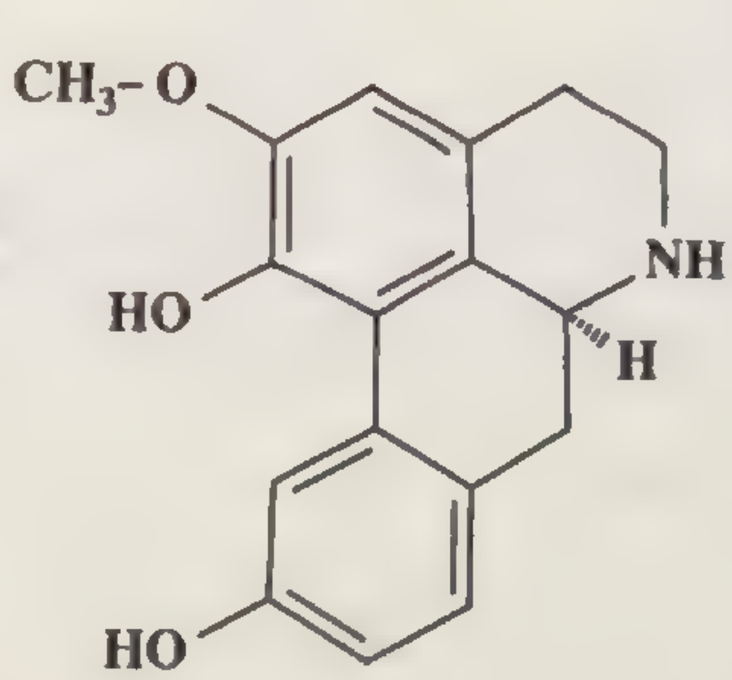


virosecurinine (25)

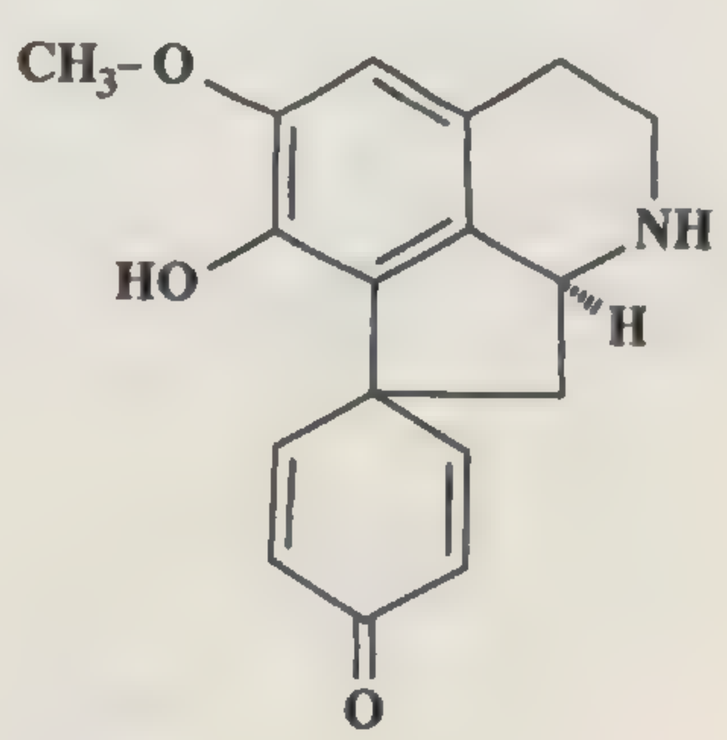
FIGURE. Continued.



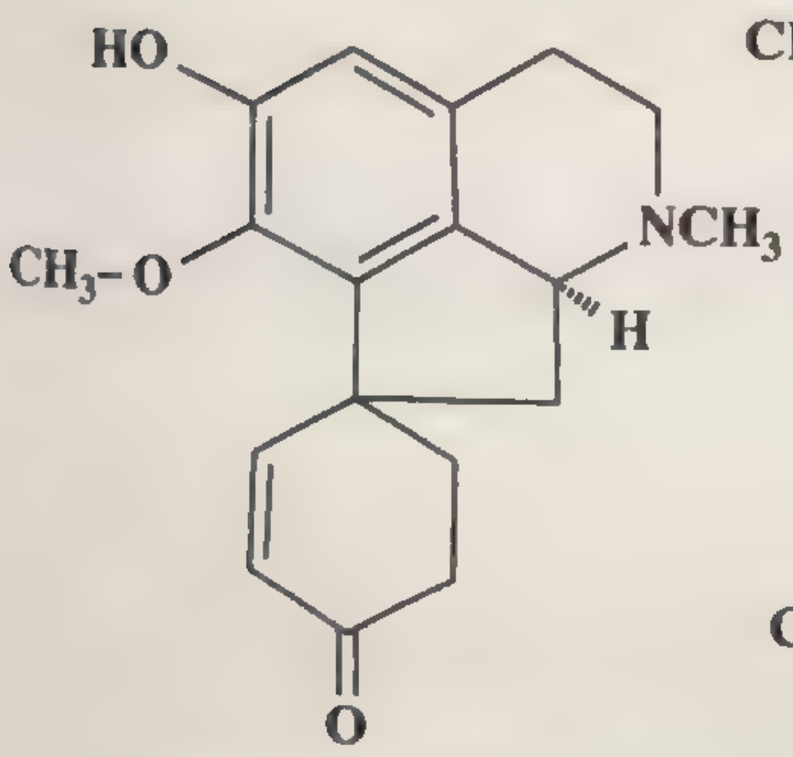
(+)-glaucine (16)



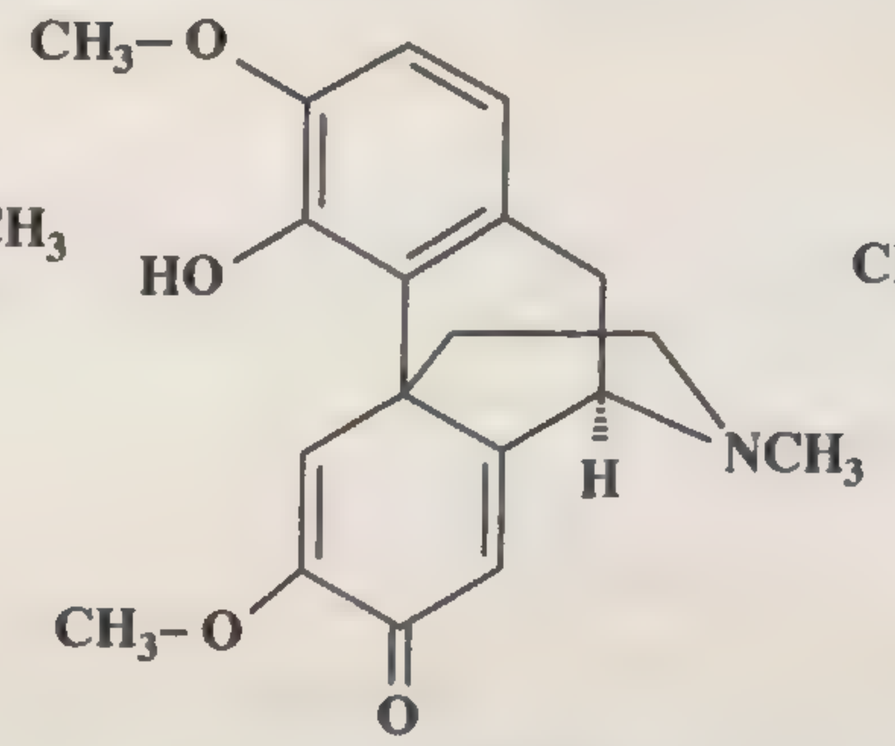
sparsiflorine (17)



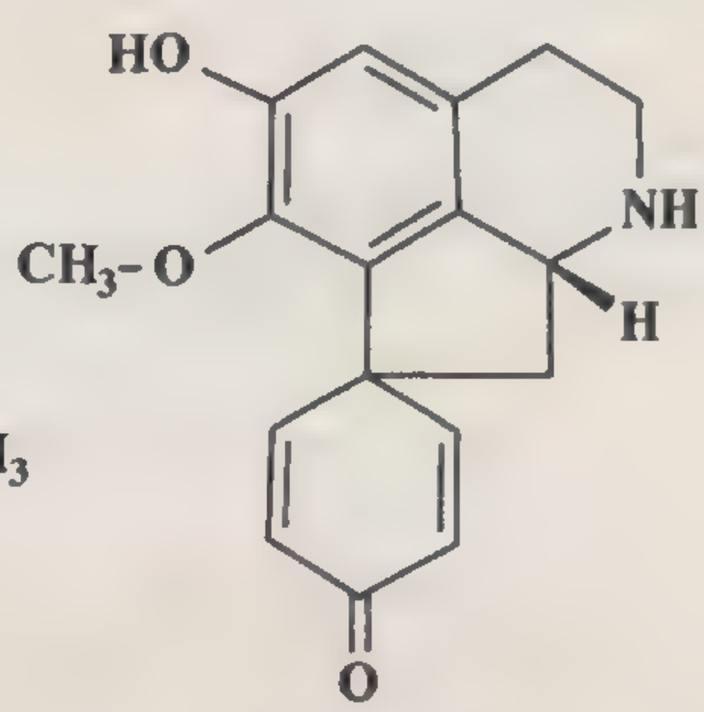
crotsparine (18)



(+)-linearisine (20)



salutaridine (21)



(+)-crotonosine (19)

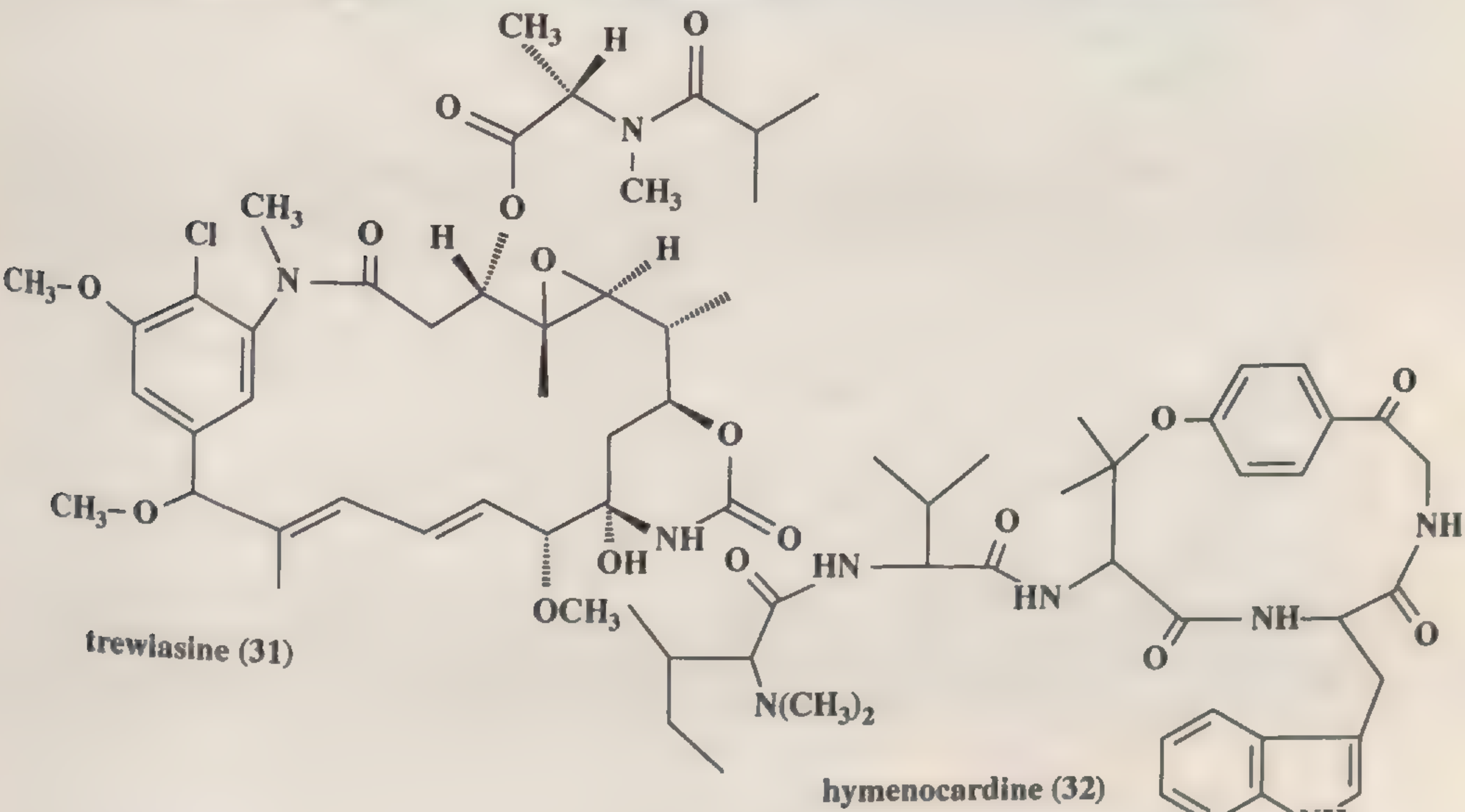
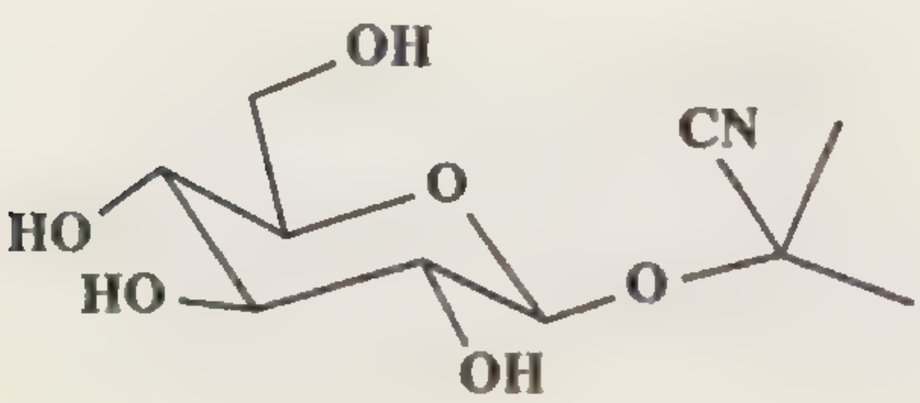
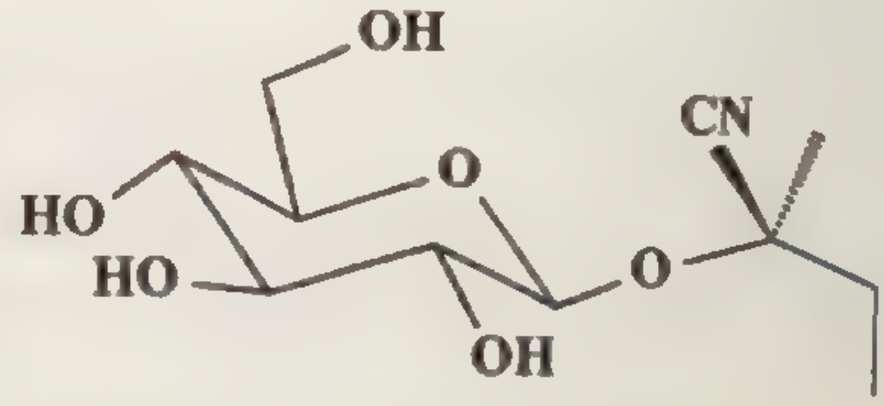


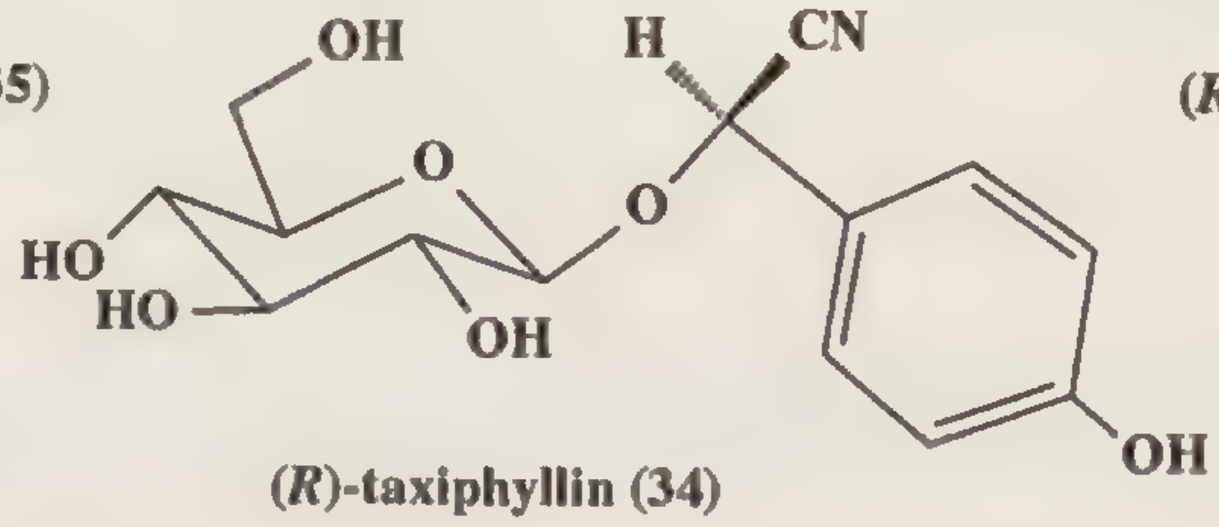
FIGURE. Continued.



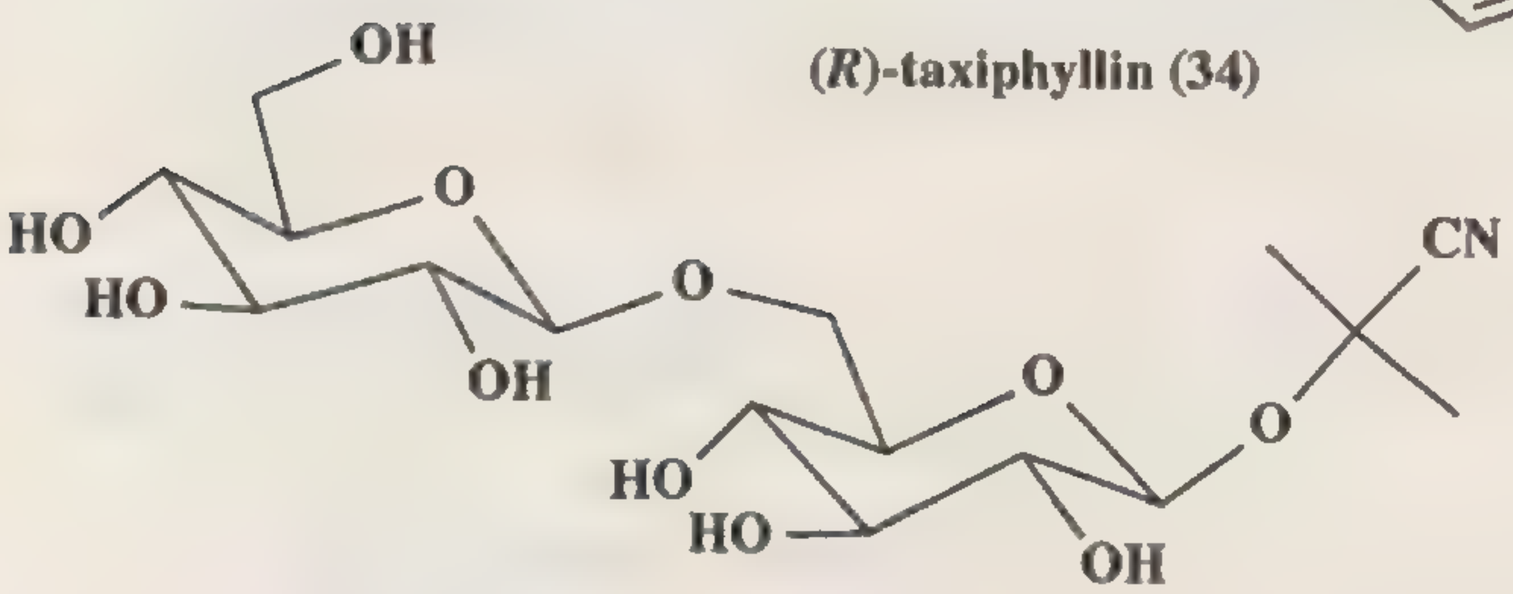
linamarin (35)



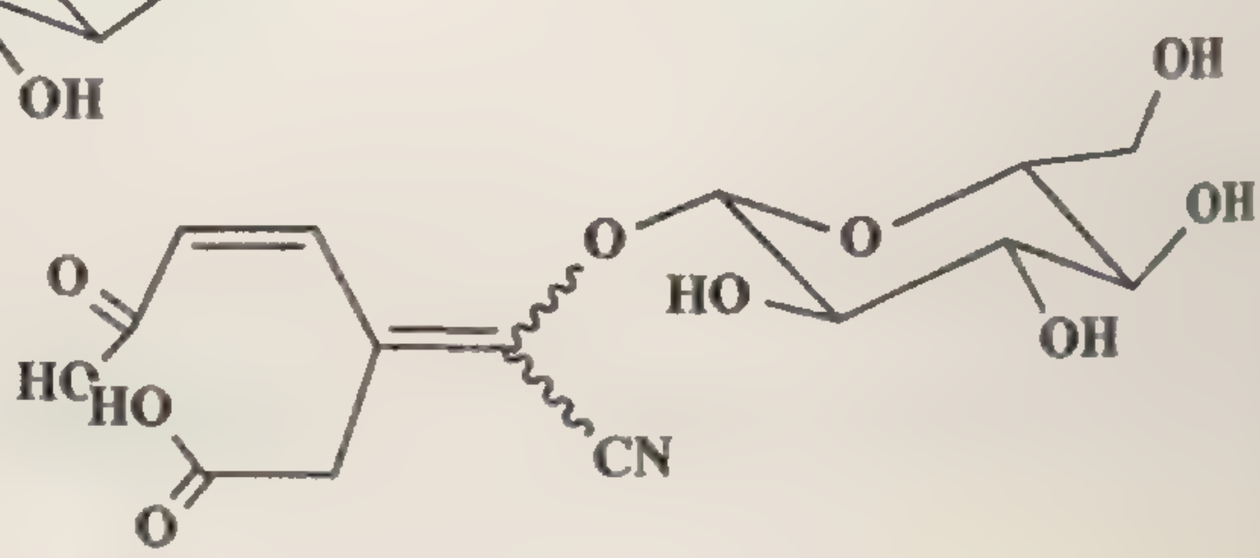
(*R*)-lotaustralin (36)



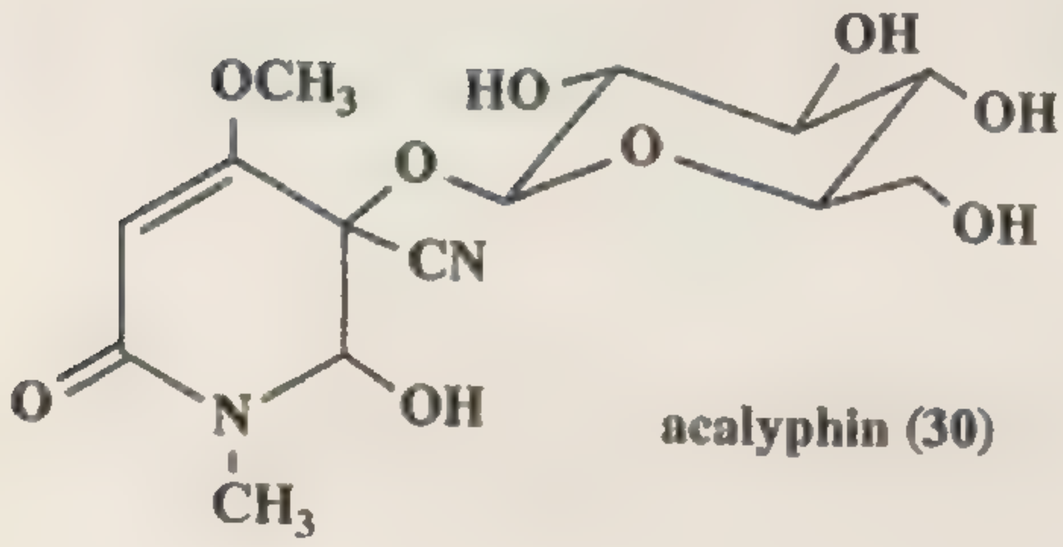
(*R*)-taxiphyllin (34)



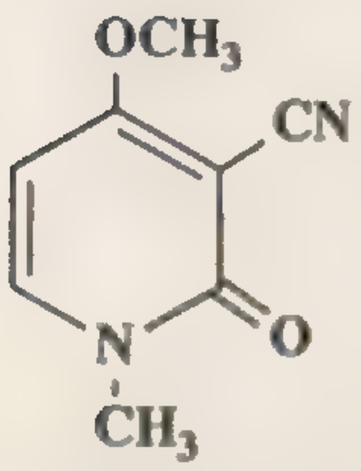
linustatin (37)



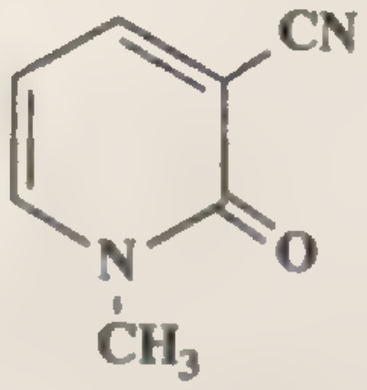
triglochinin (33)



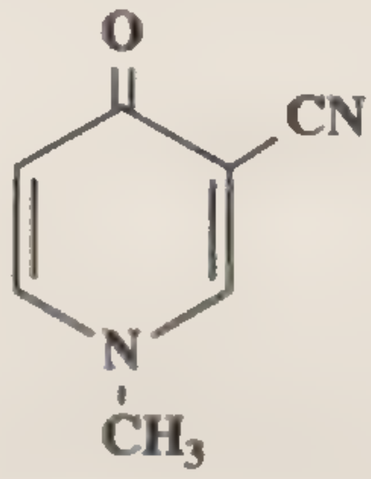
acalyphin (30)



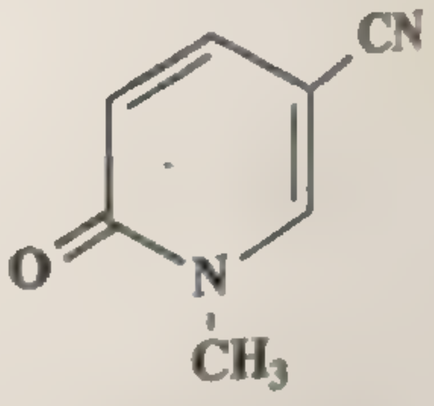
ricinine (26)



ricinidine (28)

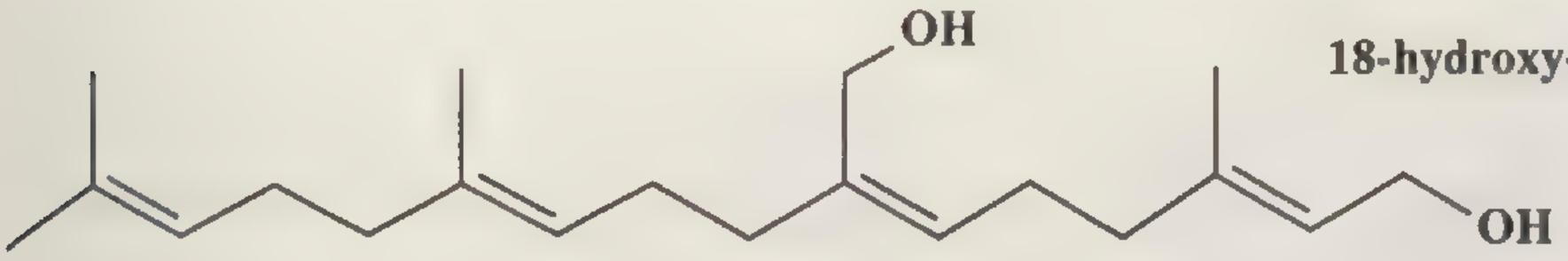


mallorepine (29)

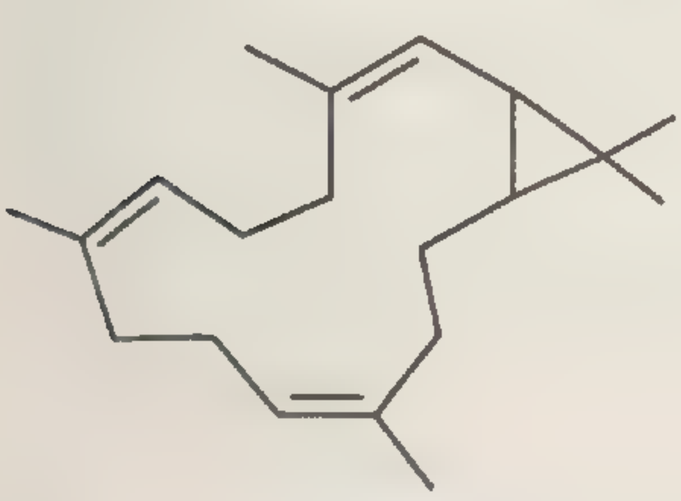


nudiflorine (27)

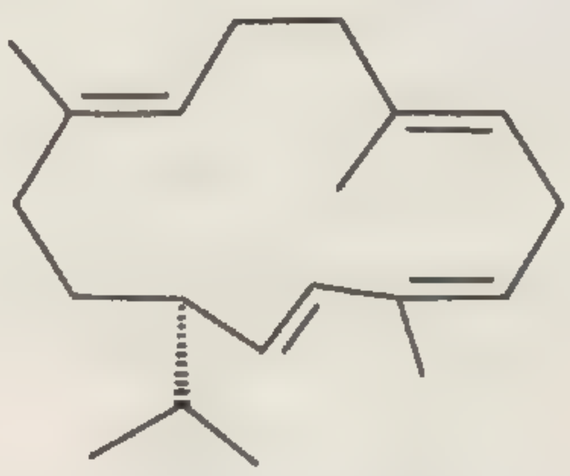
FIGURE. Continued.



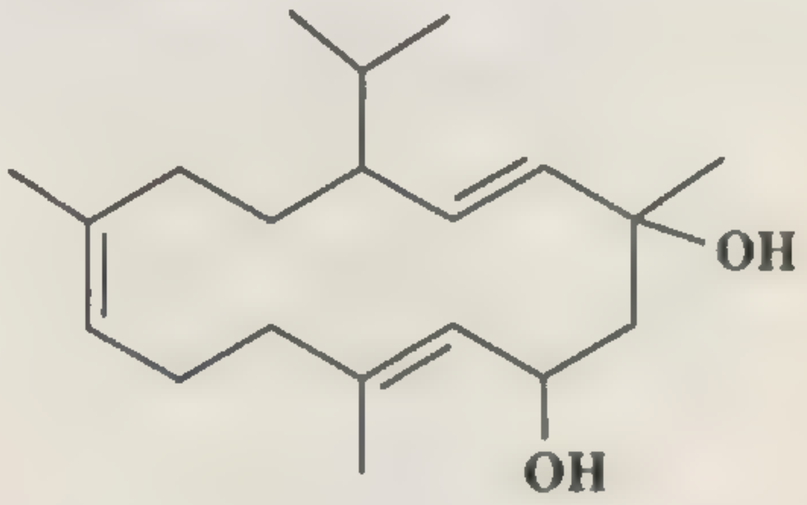
18-hydroxy-6-Z-geranylgeranyiol (38)



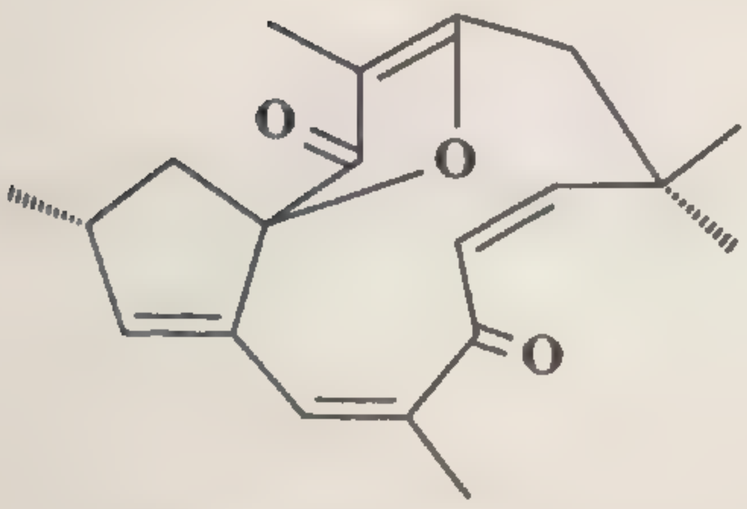
casbene (41)



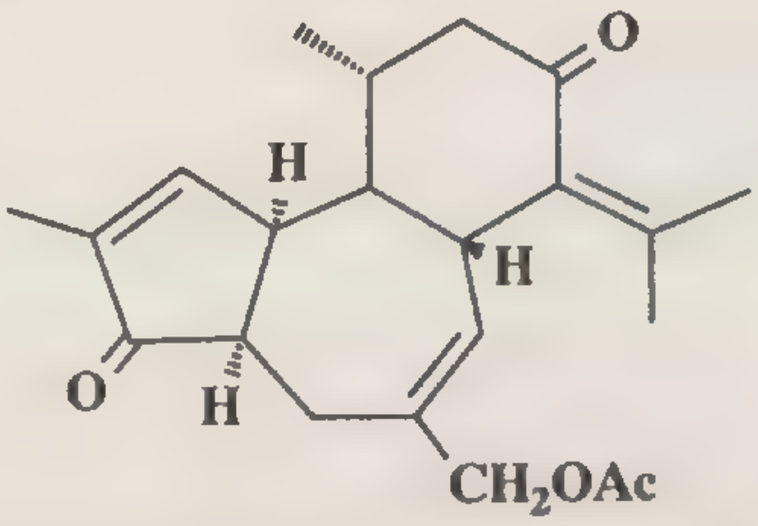
cembrene (39)



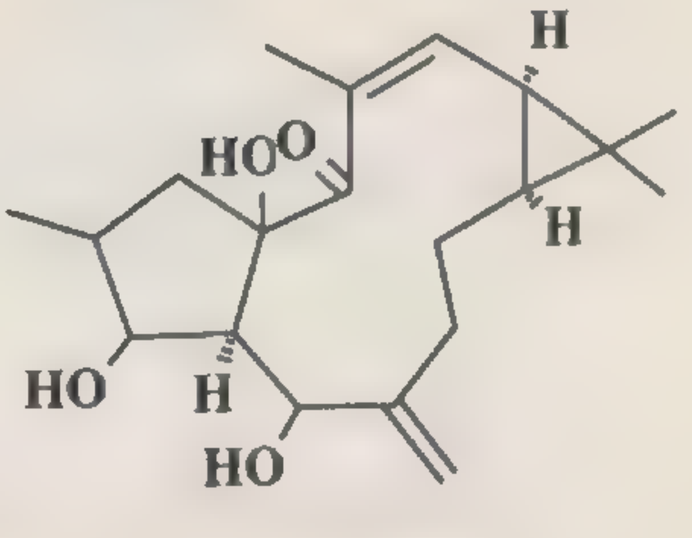
4,8,13-duvatrien-1,3-diol (40)



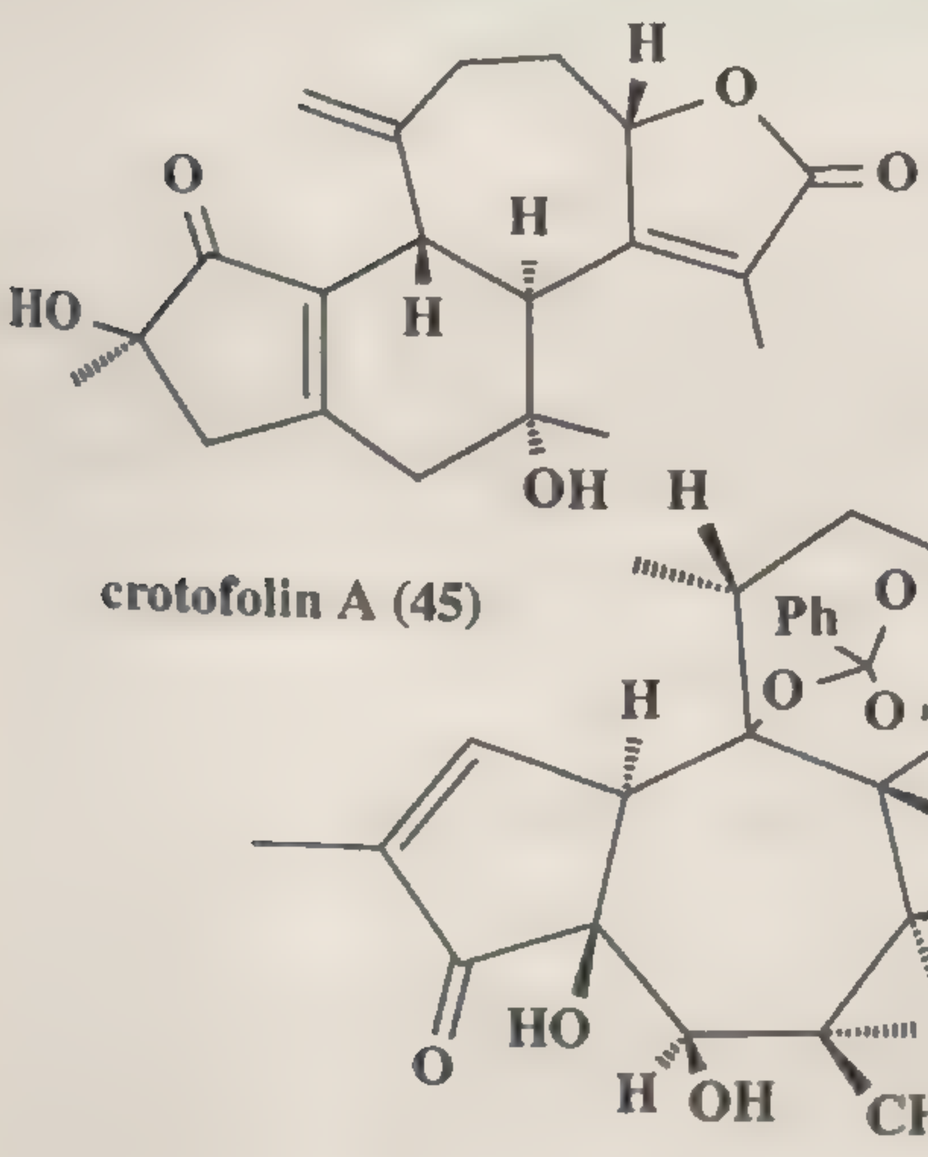
jatrophone (42)



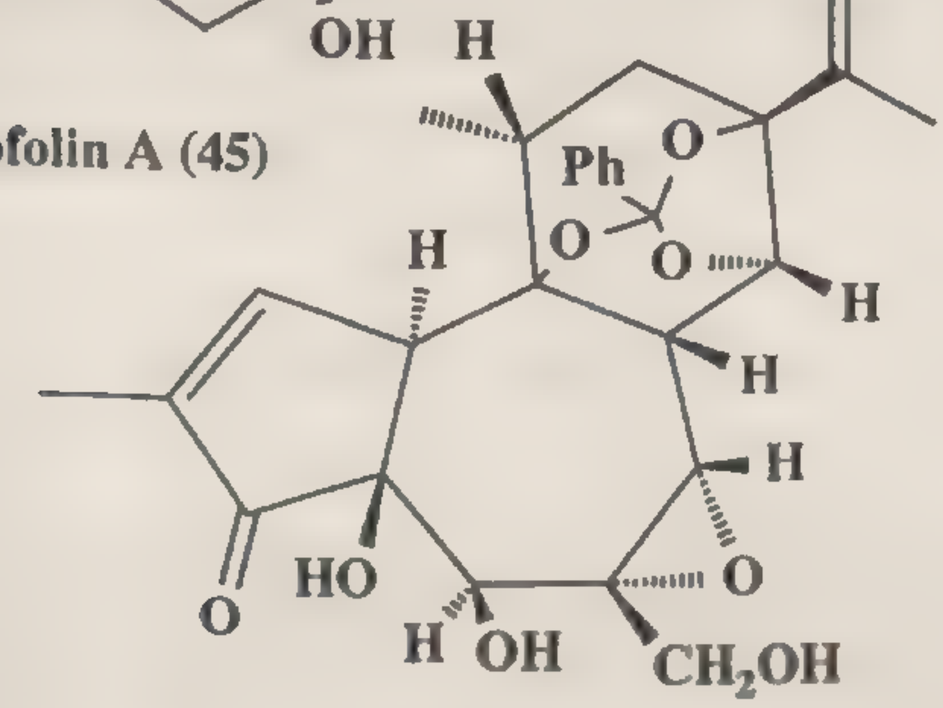
13,15-seco-4,12-dideoxy-4α-phorbol-20-acetate
(a rhamnifolane derivative) (43)



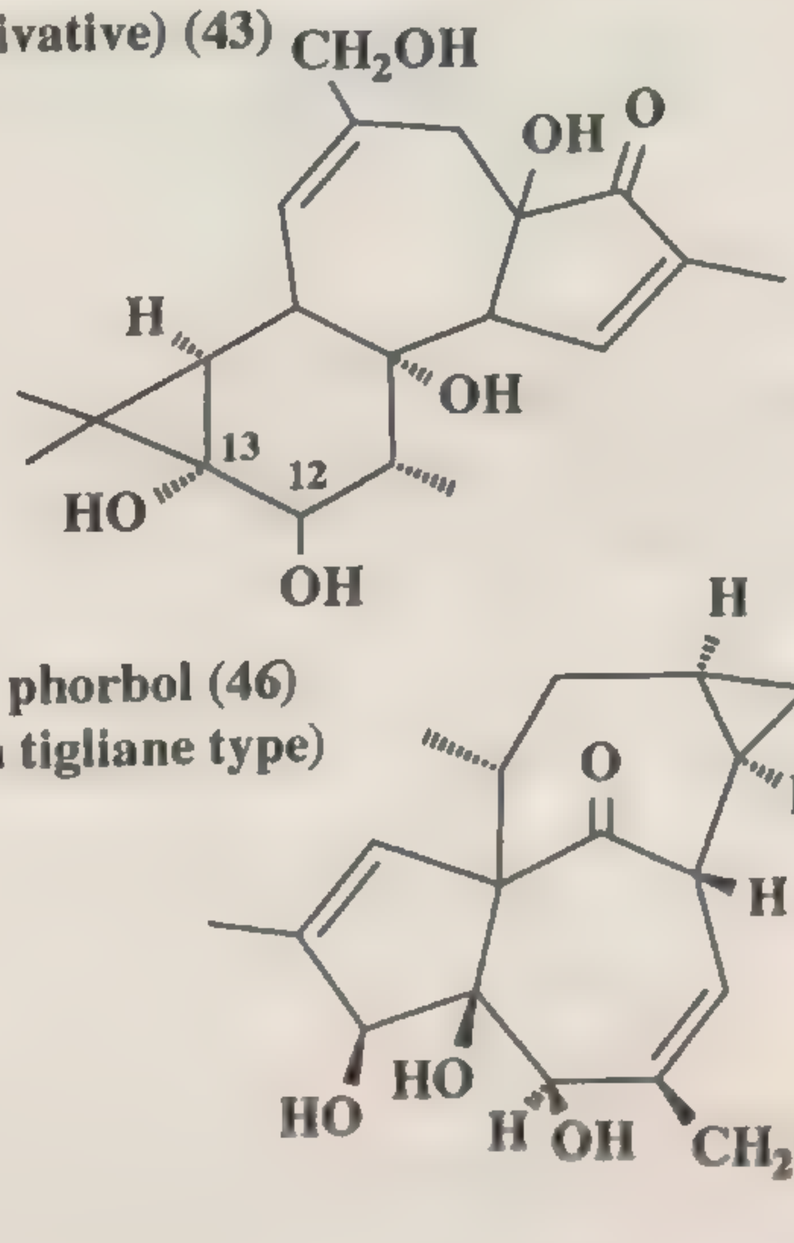
lathyrol (44)



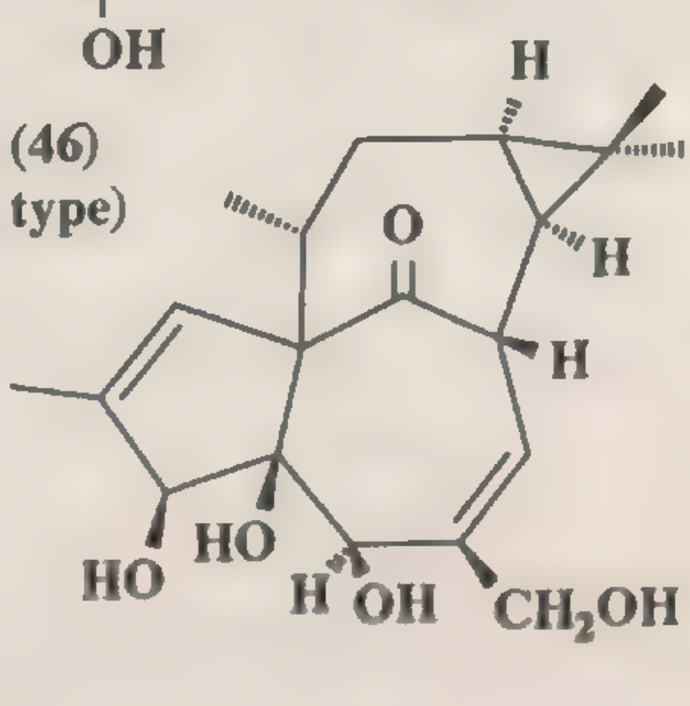
crotofolin A (45)



daphnetoxin (48)

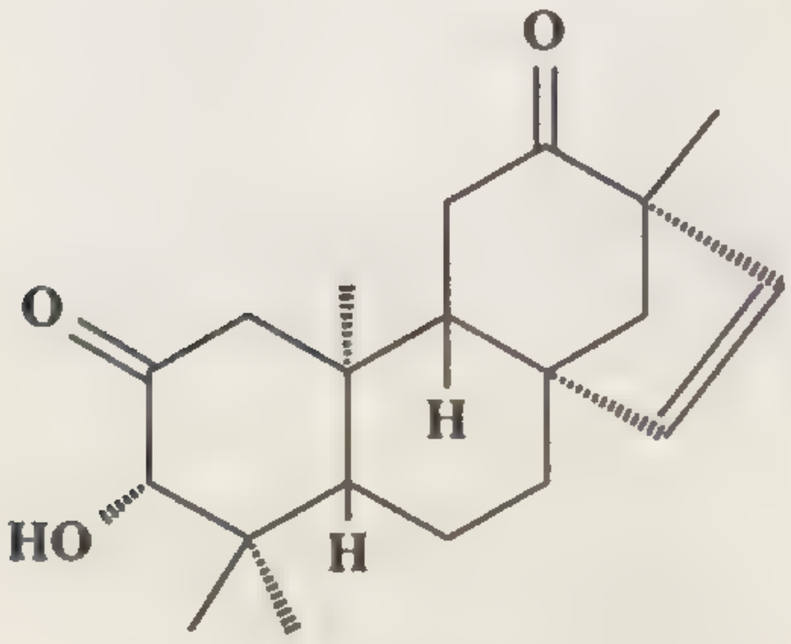


phorbol (46)
(a tigliane type)

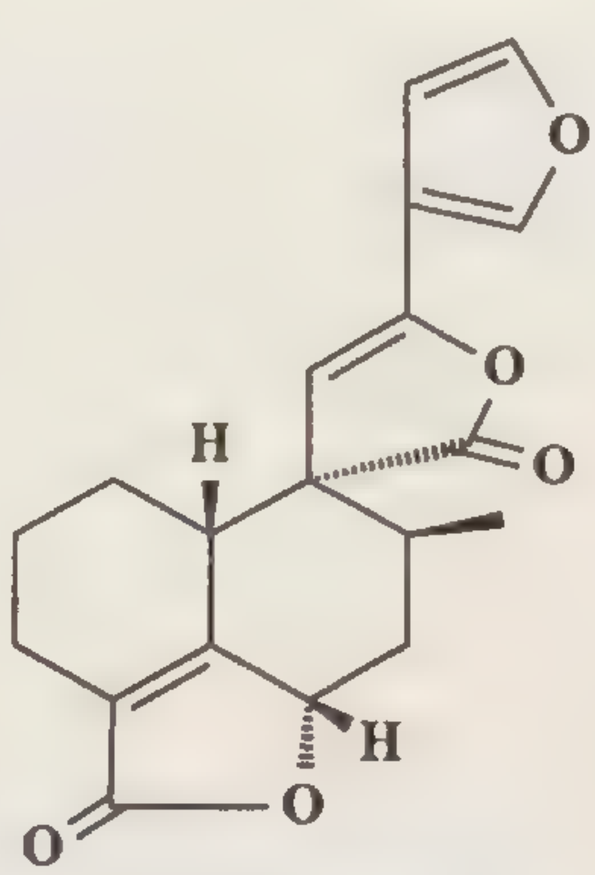


ingenol (47)

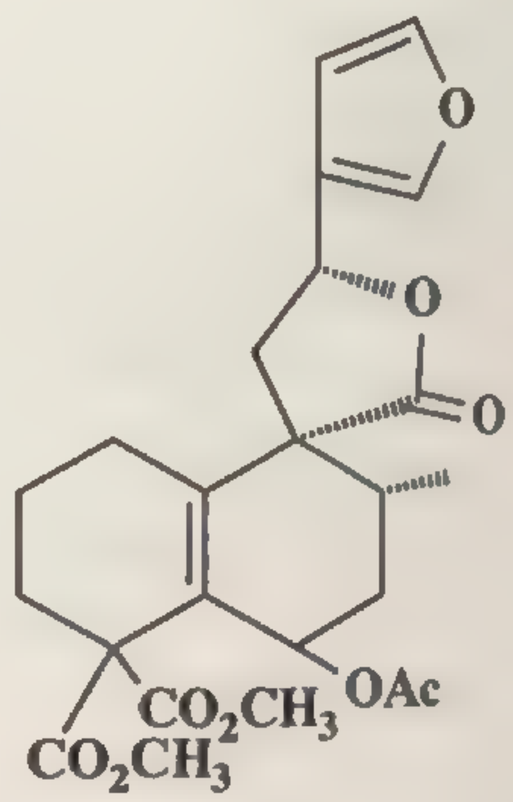
FIGURE. Continued.



ent-3β-hydroxybeyer-15(16)-ene-2,12-dione (50)



isocrotocaudin (51)



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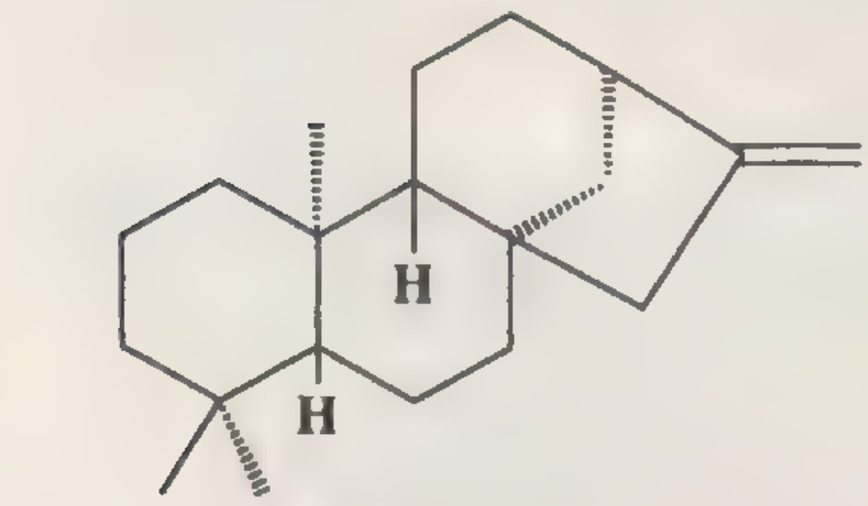

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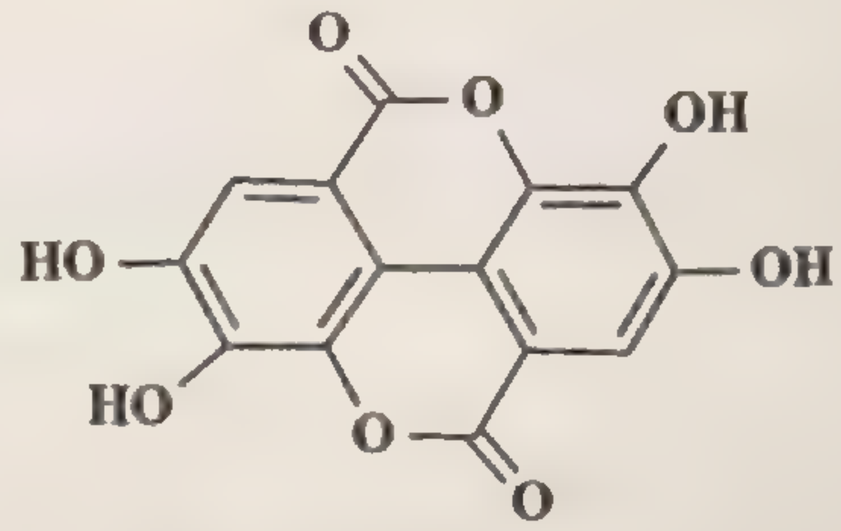

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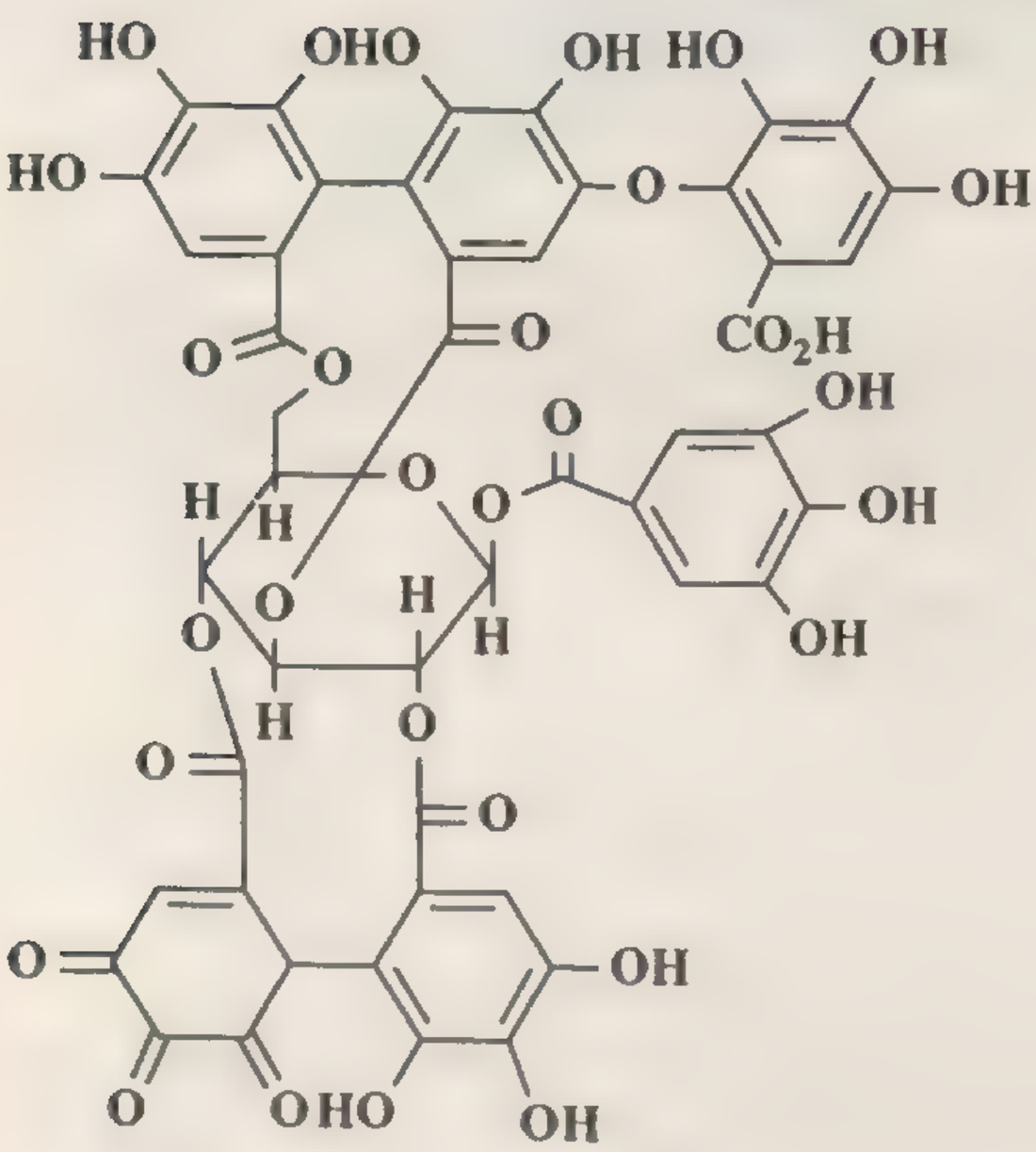

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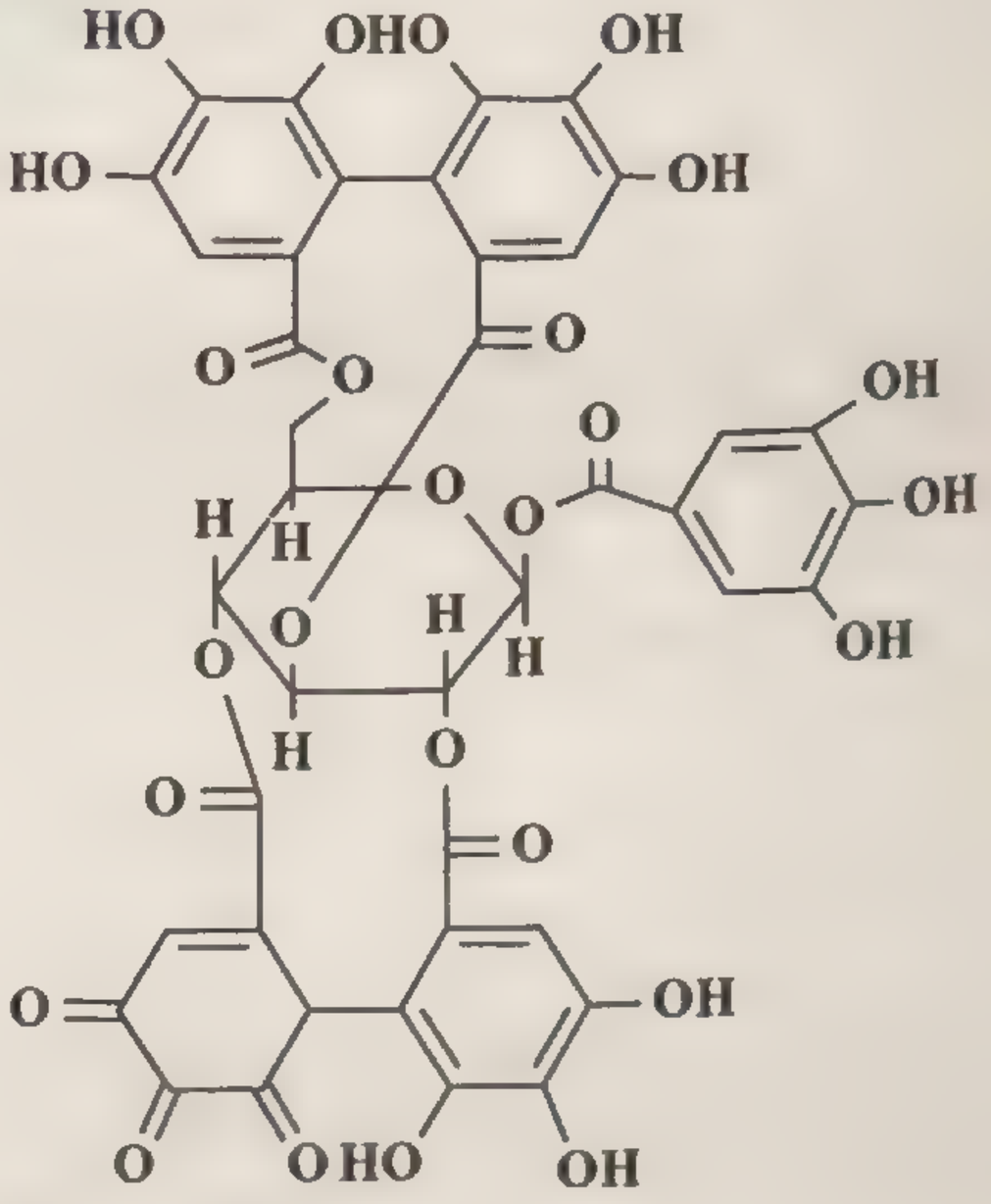

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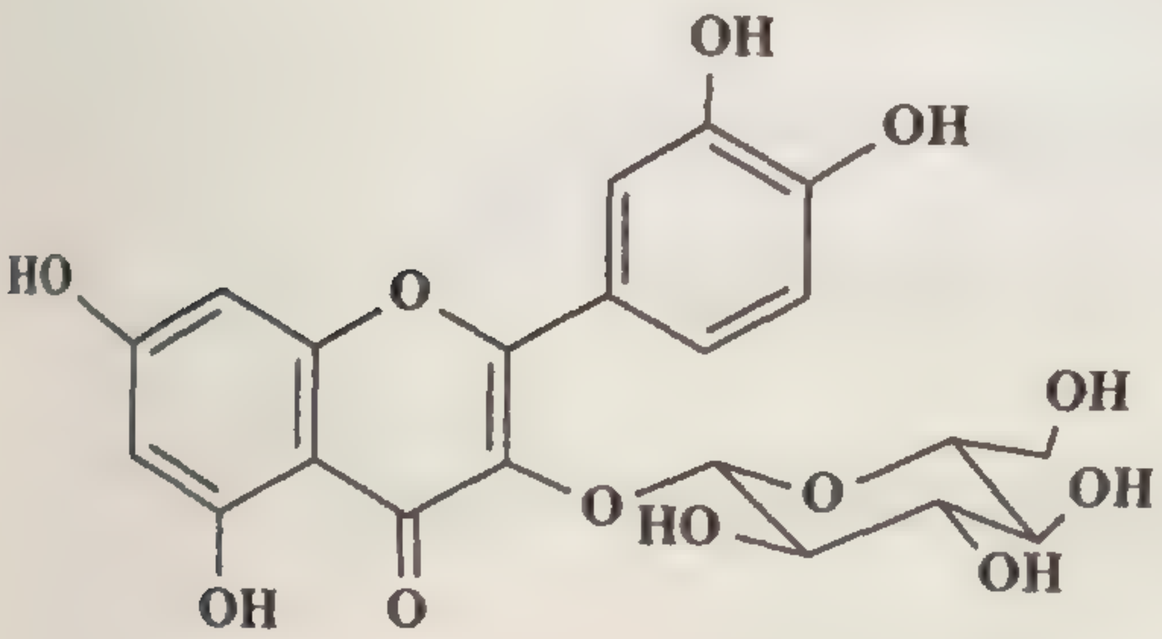

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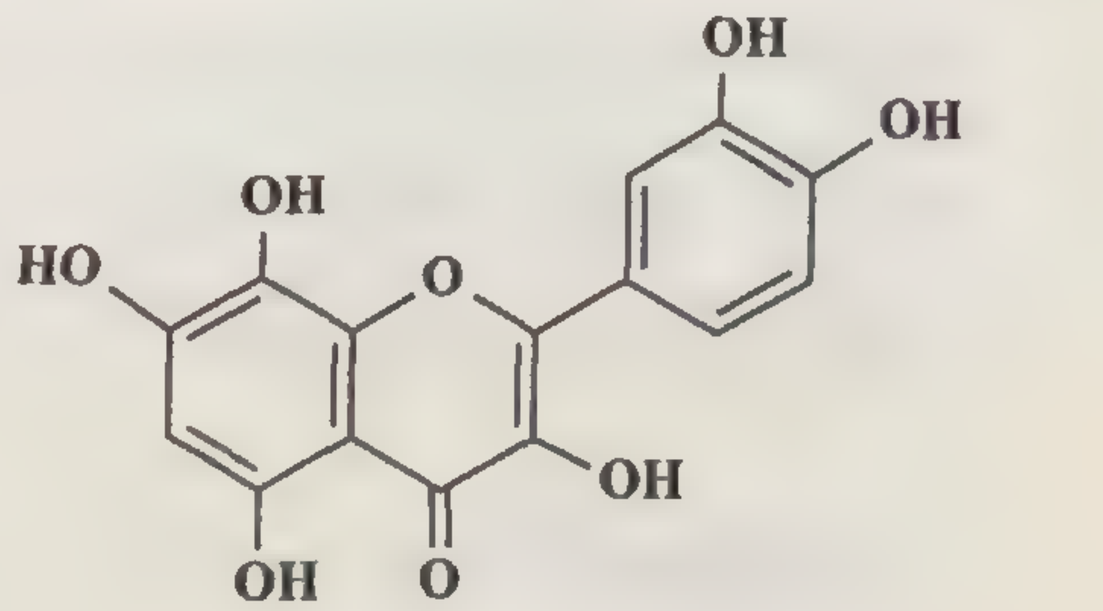

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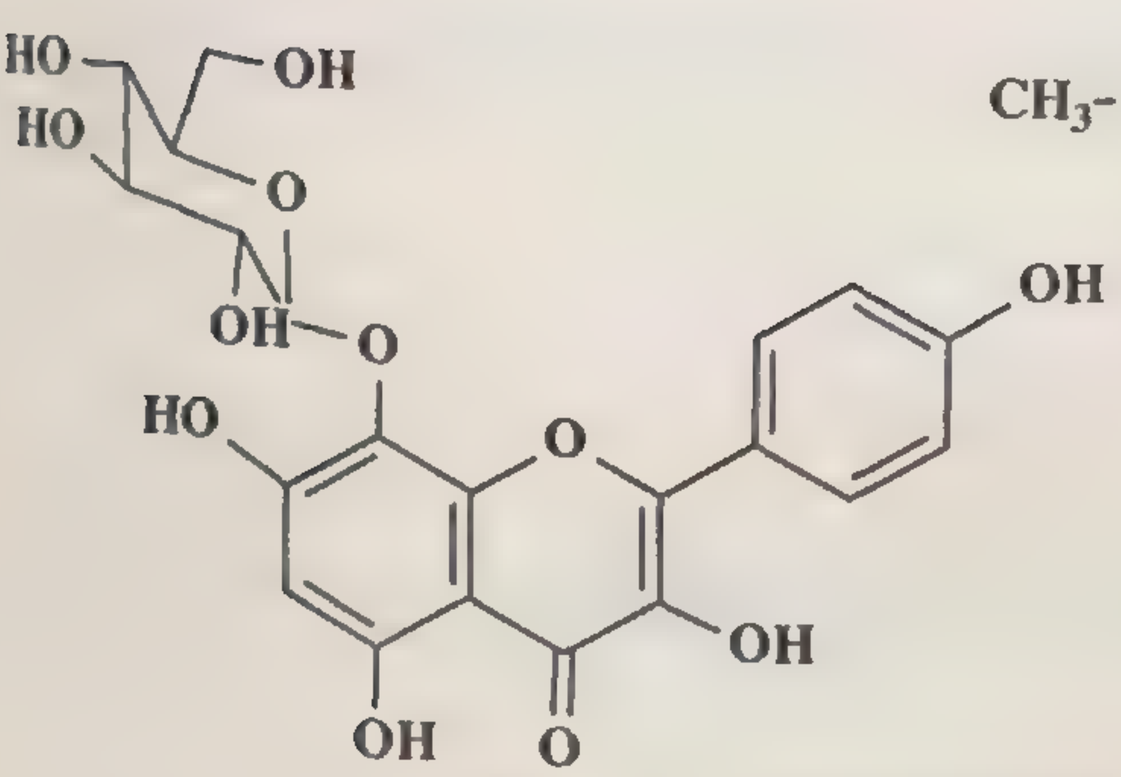

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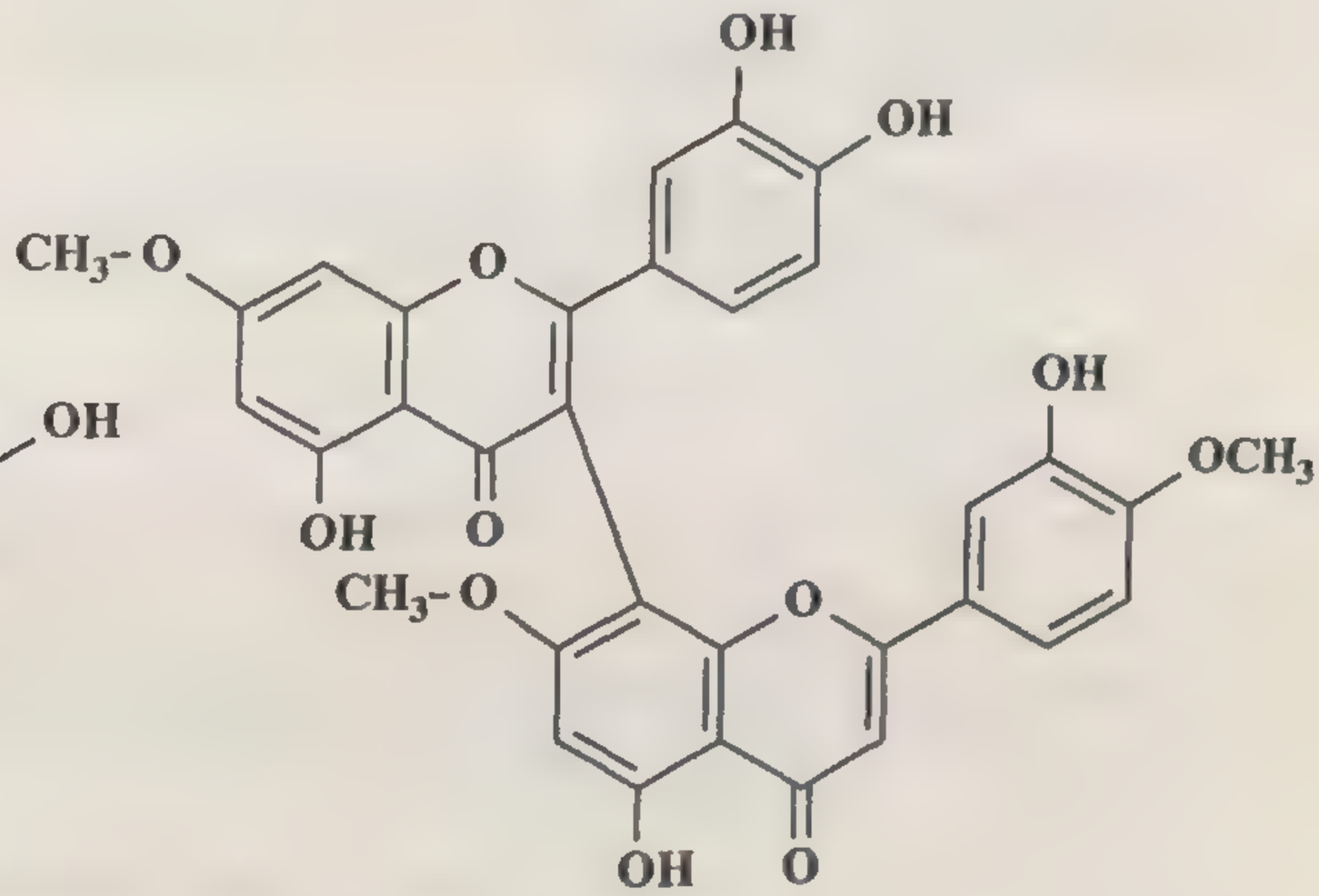

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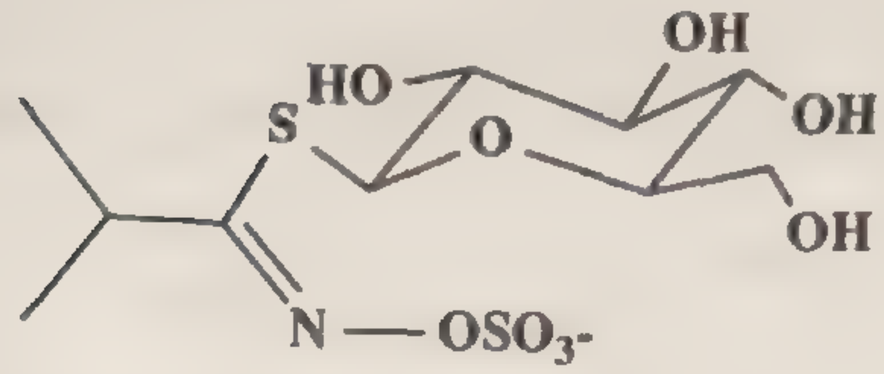

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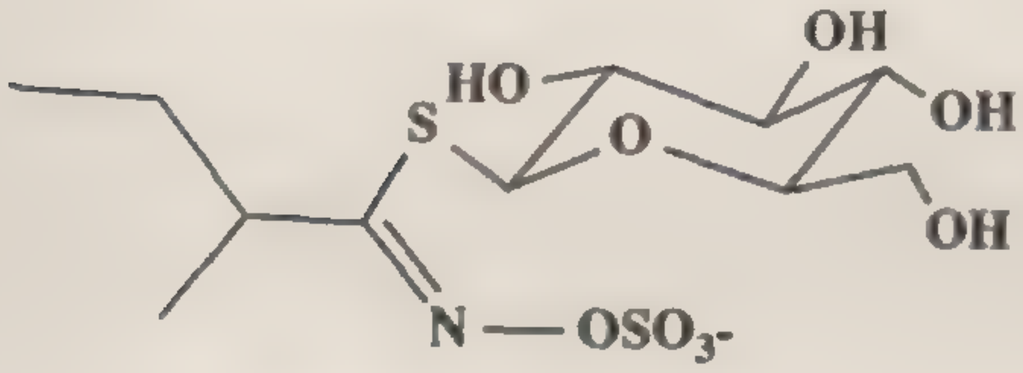

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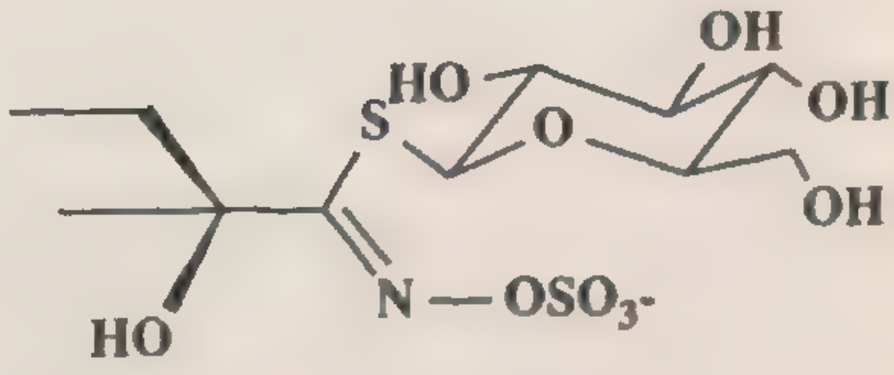

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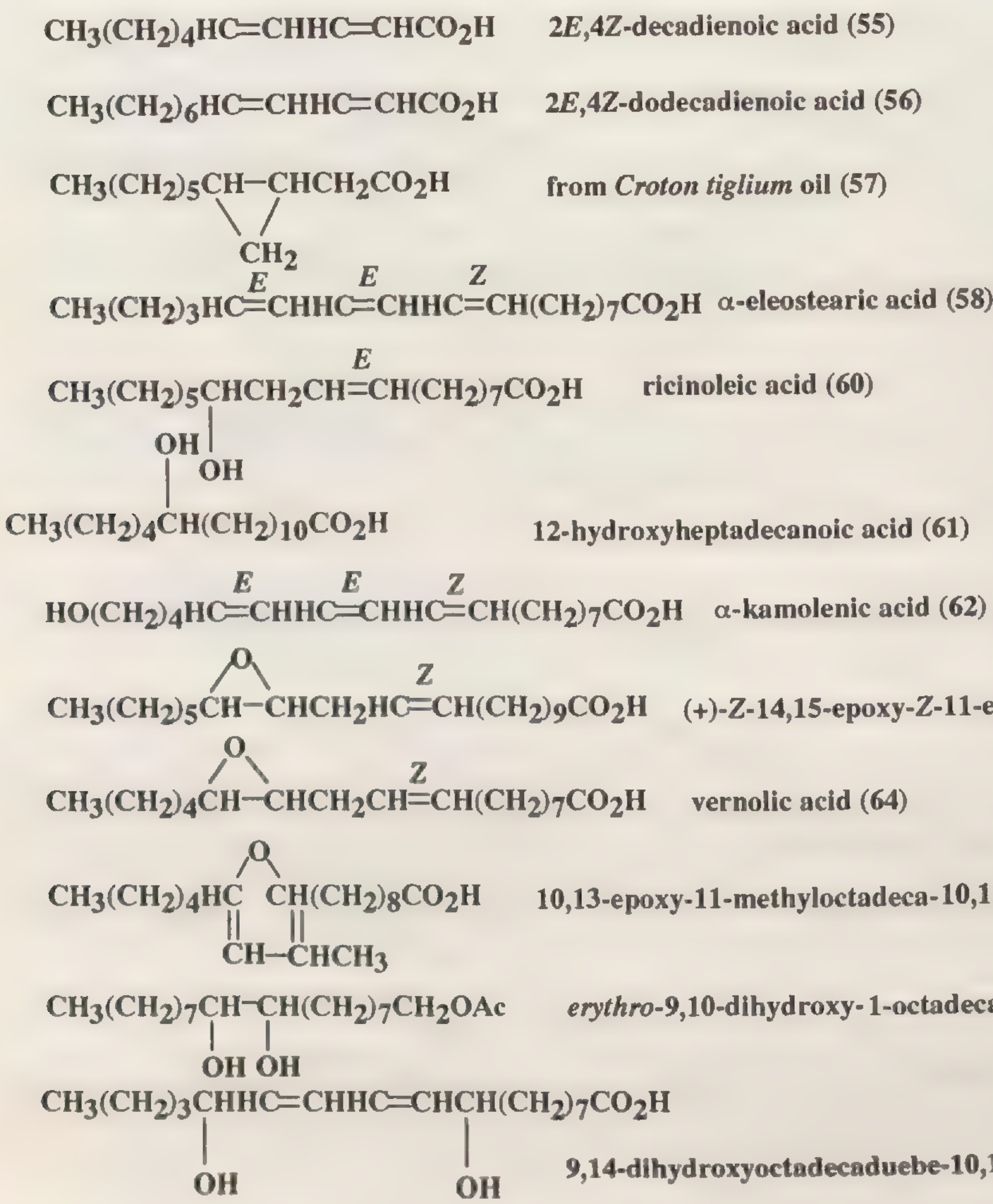

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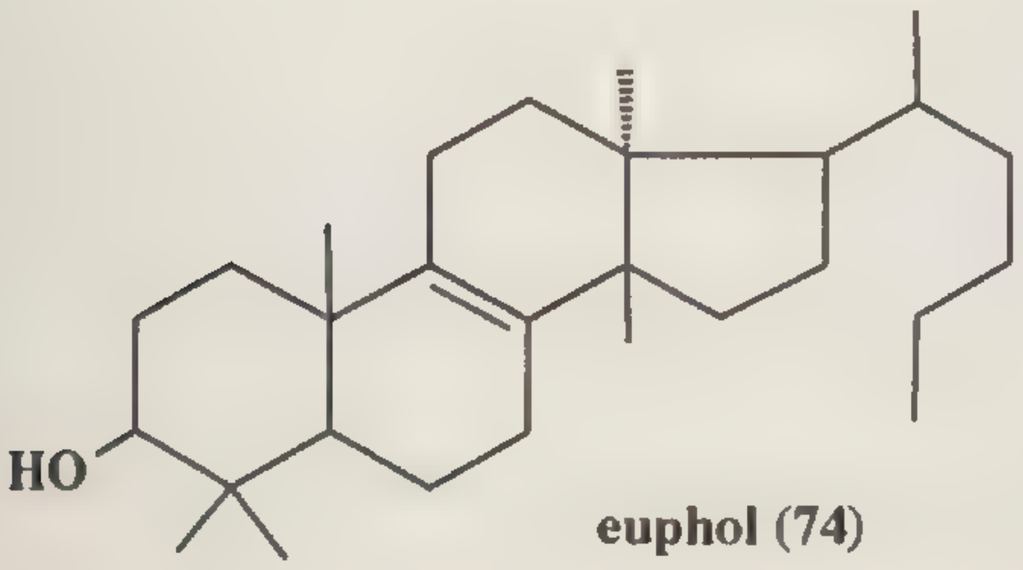

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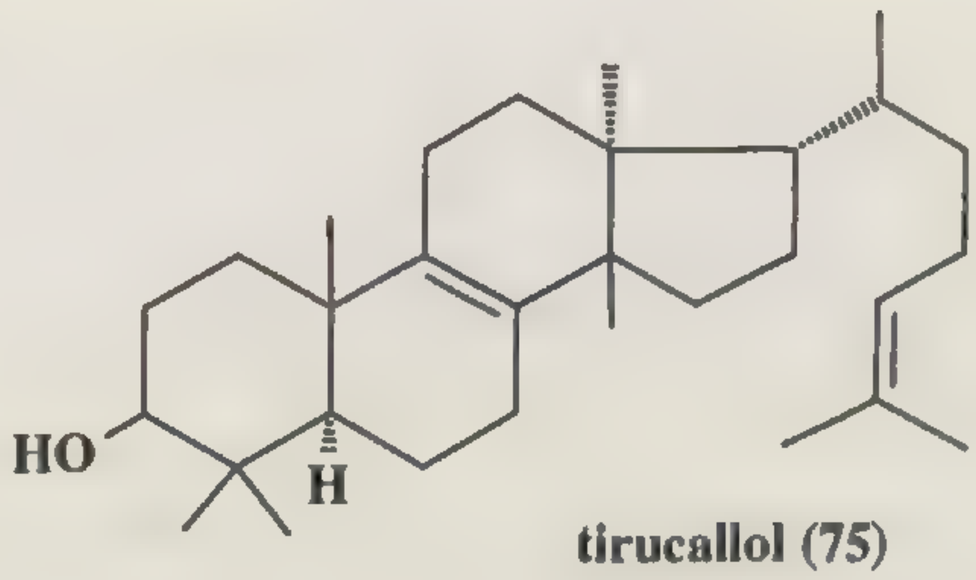

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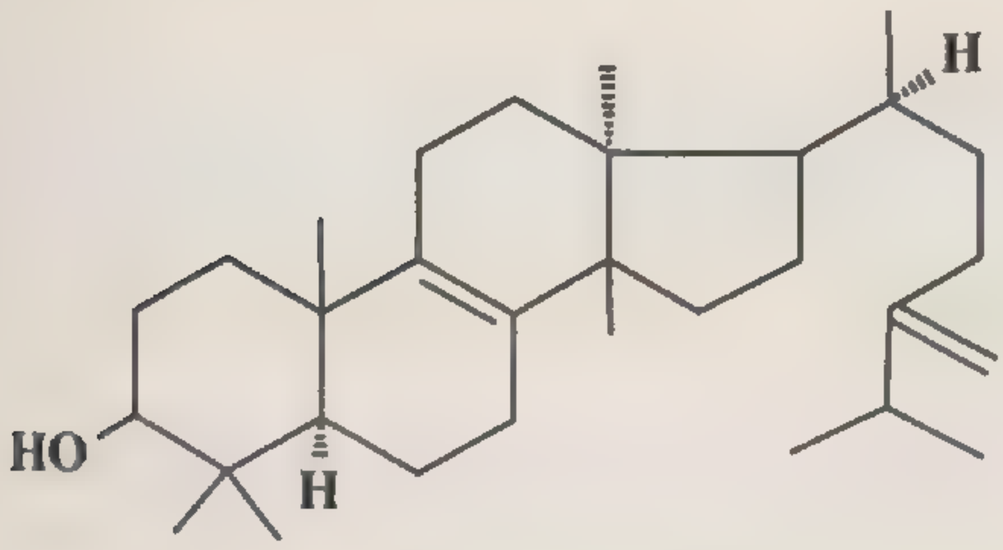

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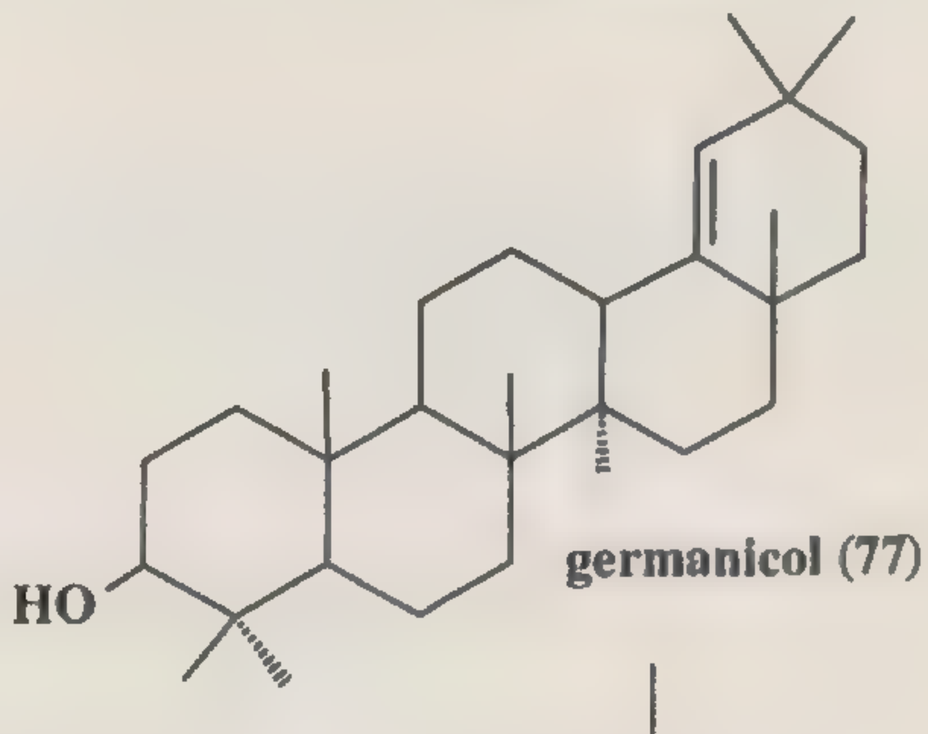

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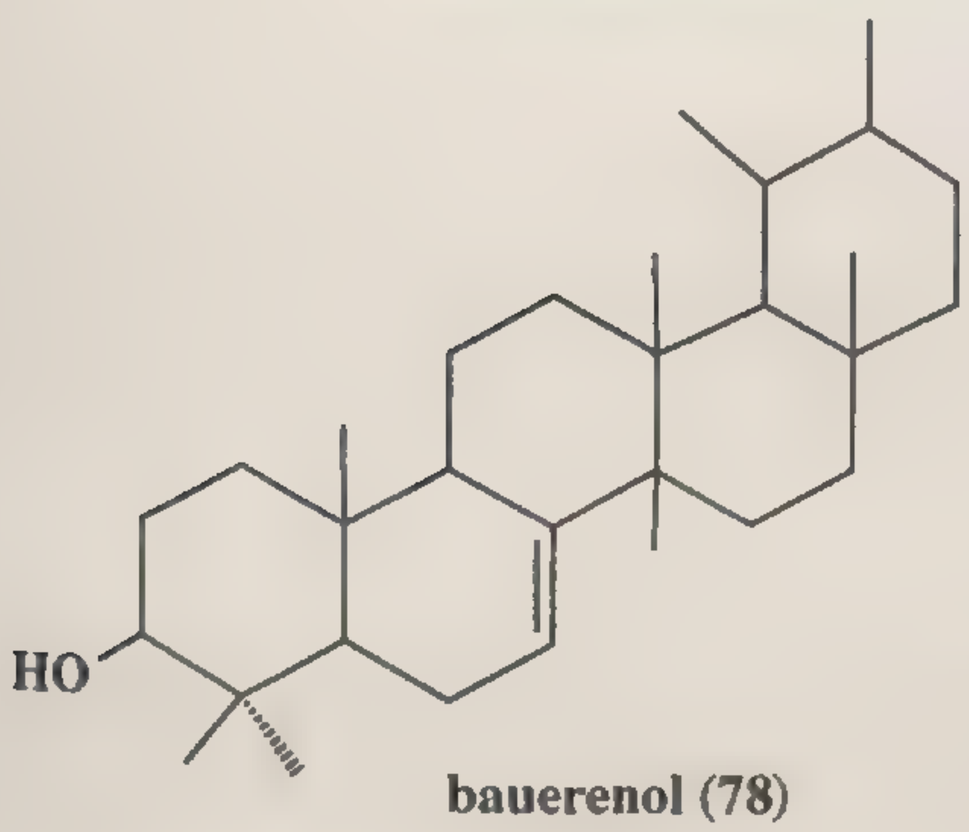

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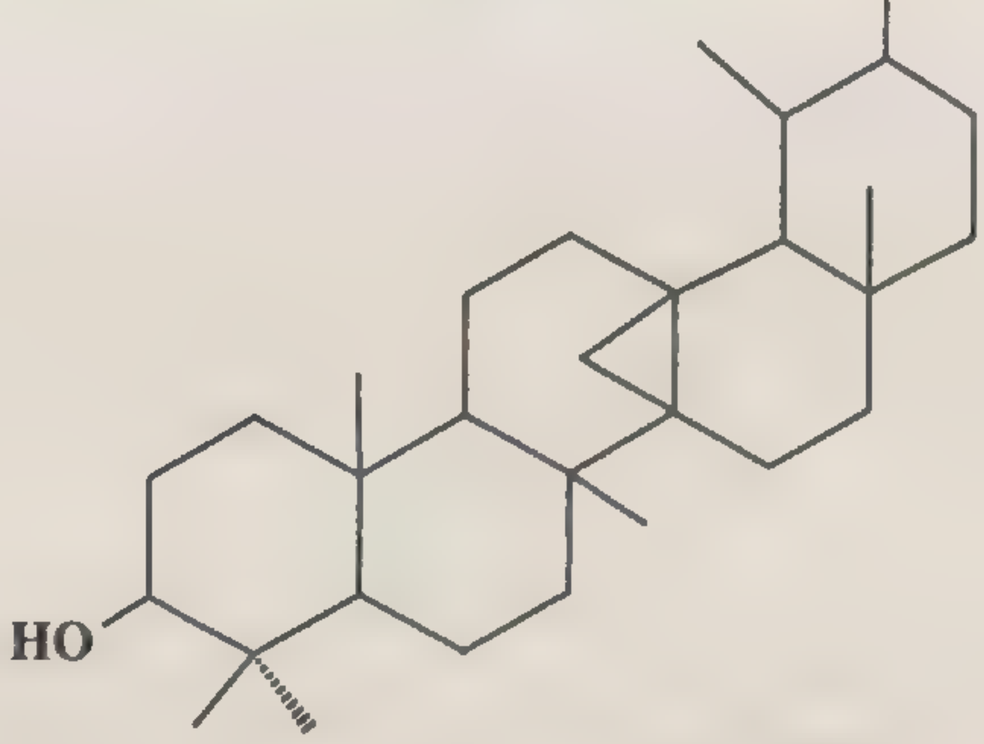

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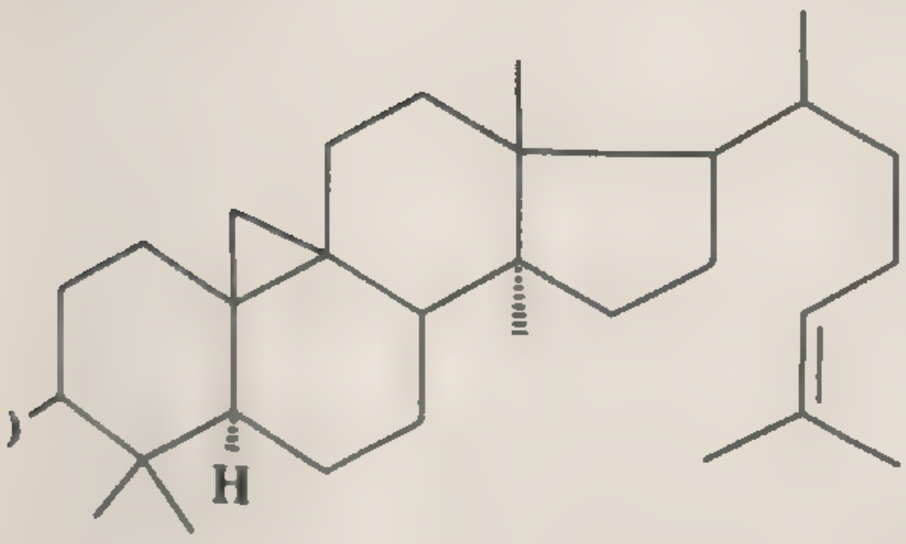
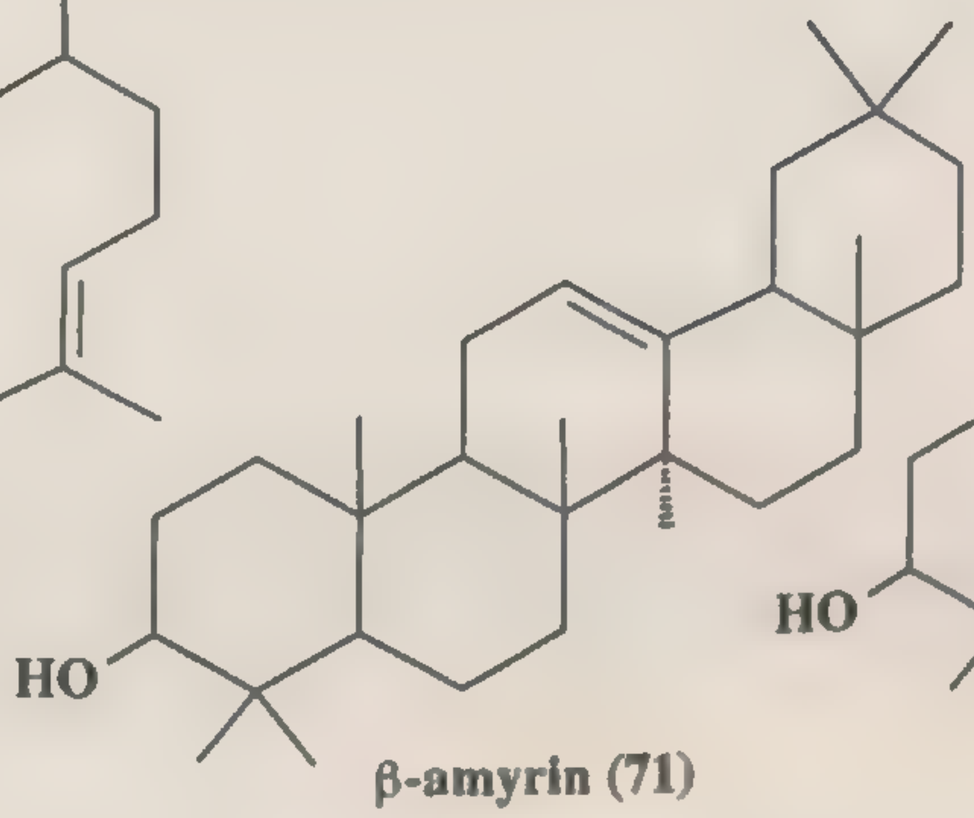
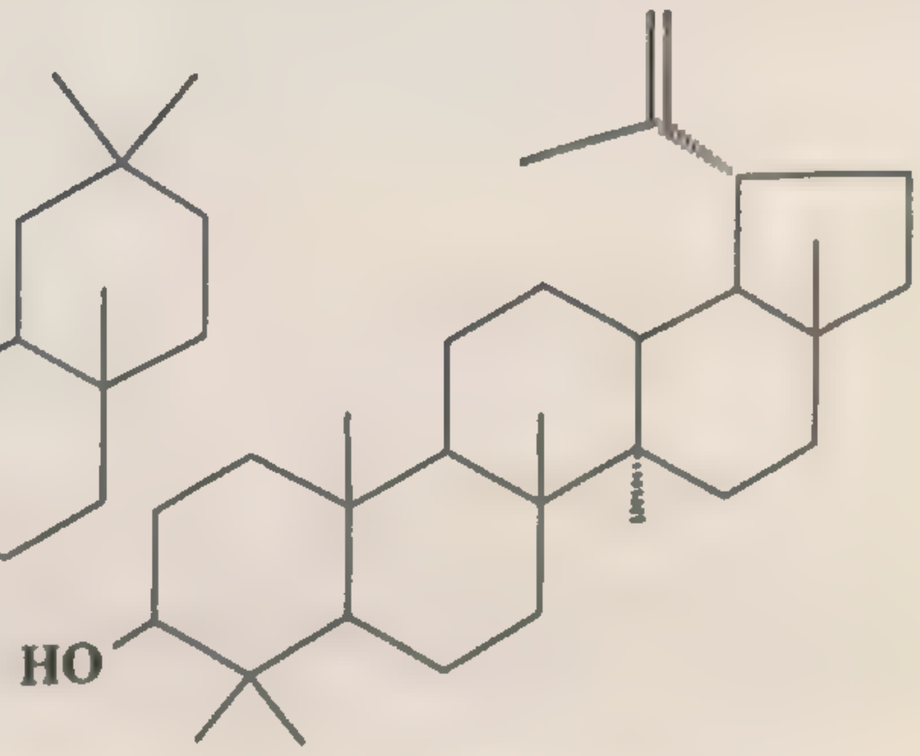


cycloartenol (73)



β-amyrin (71)



lupeol (72)

FIGURE. Continued.

Volume 81, Number 2, pp. 145–402 of the ANNALS OF THE MISSOURI BOTANICAL GARDEN
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Annals of the Missouri Botanical Garden 80(2) (Spring 1993). This symposium, the 38th Annual Systematics Symposium of the Missouri Botanical Garden (held 4-5 Oct. 1991, in St. Louis, Missouri), discusses the value and future necessity of assimilating diverse biological information into new and broader syntheses, taking advantage of computer-based data-management systems. 41 pages (entire issue 230 pages). $35.00, plus postage.

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Annals of the Missouri Botanical Garden 80(3) (Summer 1993). Fourteen papers plus an appendix containing voucher and sequence data. This collection of papers, organized by Douglas E. Soltis and Mark W. Chase, presents the first in-depth molecular phylogenetic analysis of seed plants in general, and angiosperms in particular. Investigators throughout the world involved in *rbc*L sequencing studies contributed their unpublished sequences for a broad phylogenetic analysis. 235 pages. $40.00, plus postage.

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Cover illustration. *Petrea sulphurea* M. J. Jansen-Jacobs, by Phyllis Bick.

Annals of the Missouri Botanical Garden 1994

Volume 81
Number 3

Volume 81, Number 3
Summer 1994

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Missouri Botanical Garden

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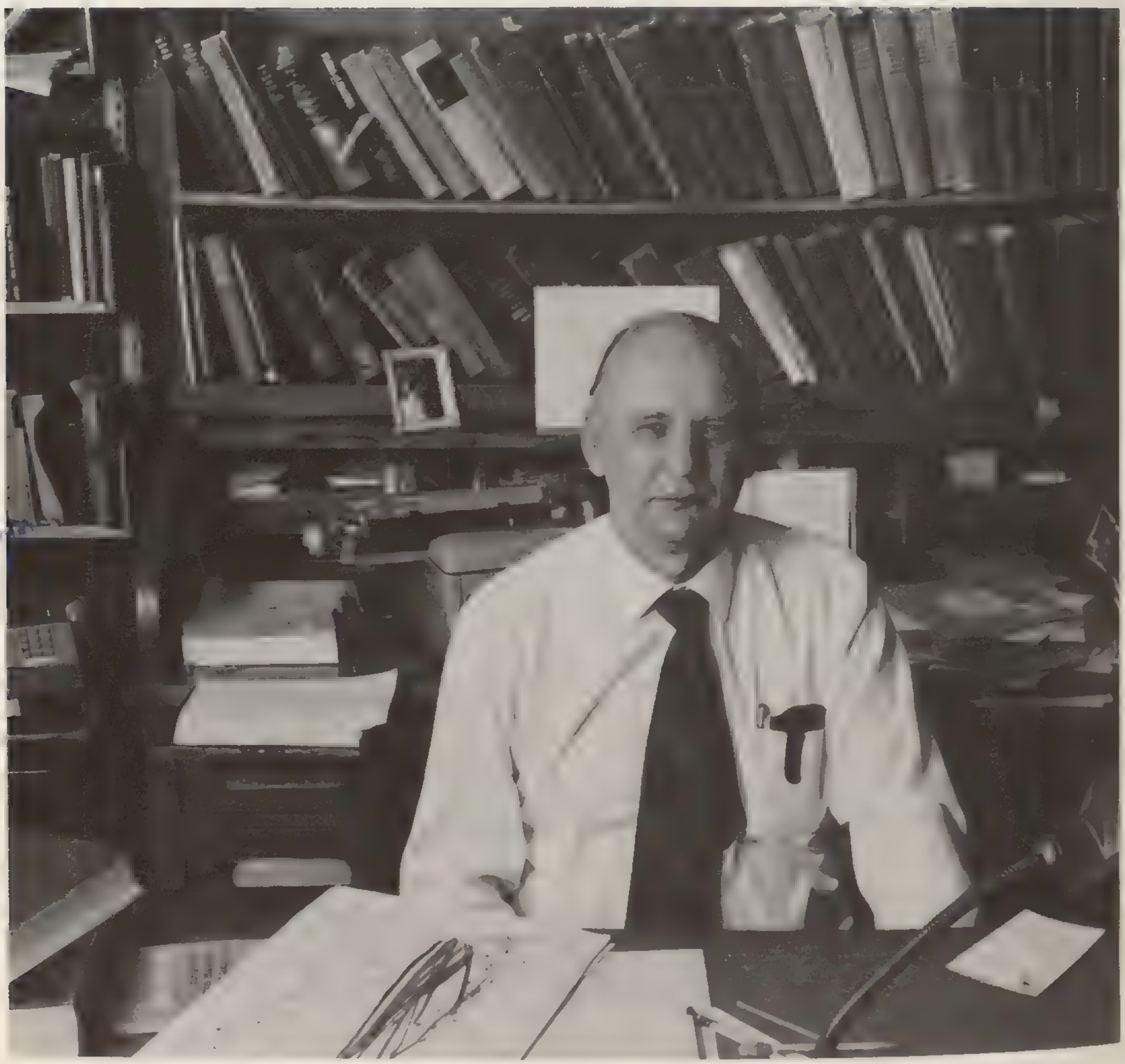

Arthur Cronquist
1919–1992

Volume 81
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ORIGIN AND RELATIONSHIPS OF THE MAJOR PLANT GROUPS: DEDICATION AND INTRODUCTION[1]

P. Mick Richardson[2]

Art Cronquist surely knew more about the origin and relationships of plant groups than anyone who has ever lived. It is with great pleasure that we dedicate this symposium to him; I am sure that he would have enjoyed it. You might well think that he would have objected to all the cladograms, and you may be surprised to discover that you are wrong about this. I myself almost fell off my chair in disbelief when, deep inside the medieval Castel dell'Ovo in the Bay of Naples and barely three years after his botanical critique of cladistics (Cronquist, 1987), he uttered the words, "We can usefully think in terms of apomorphies and plesiomorphies, and develop tentative cladograms . . ." (Cronquist, 1990). Of course, I do not wish to imply that Art became a cladist. However, he was always open to new ideas about the relationships of one group of plants to another, and if the cladists were the ones producing the new ideas, then Art thought that they deserved to be listened to. Yes, he would have enjoyed the symposium.

The symposium showed how far we have advanced since Lynne Parenti published the controversial first phylogenetic reconstruction of the land plants based upon Hennigian principles (Parenti, 1980). It is interesting to note that arguments about homologous characters (Young & Richardson, 1982) continued. The papers presented at the symposium, most of which are also published in this issue, covered a diversity of topics ranging from the eukaryotic microorganisms through the angiosperms. Mitch Sogin was first on the program and discussed the rRNA-based relationships of eukaryotic microorganisms, summarized in Sogin (1991). Brent Mishler and his colleagues covered the "green algae" and the "bryophytes." Peter Crane and Paul Kenrick talked about the early diversification of the tracheophytes; for details see Kenrick & Crane (1991), Kenrick (in press), and Crane & Kenrick (The Origin and Diversification of Land Plants, in prep.). Kevin Nixon and his colleagues presented opinions about the relationships of the seed plants that differed somewhat from those put forward by Jim Doyle and his col-

[1] This and the five articles that follow it are proceedings of the 39th Annual Systematics Symposium of the Missouri Botanical Garden, Origin and Relationships of the Major Plant Groups. The symposium was held 2-3 Oct. 1992 at the Missouri Botanical Garden in St. Louis, Missouri, U.S.A.

The symposium was supported in part by the National Science Foundation under grant number BSR89-18138. I thank Mike Donoghue for help in organizing the symposium. I am also grateful to Mrs. Lucy Kluska, Arthur Cronquist's long-serving right hand and secretary, for helping me with the choice of the photograph.

[2] Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166, U.S.A.

laborators. Victor Albert, Mark Chase, and their colleagues presented a summary of the enormous amount of vascular plant *rbc*L data and warned us of some of the pitfalls in data interpretation. Finally, the after-dinner presentation was given by Michael Donoghue, who gazed knowingly into the crystal ball and boldly predicted a continued move toward a phylogenetic system of classification with the consequent elimination of familiar paraphyletic taxa. While the symposium was certainly not a eulogy for the "algae," "bryophytes," "pteridophytes," "gymnosperms," and "dicots," it emphasized the continued and growing interest in the cladistic analysis of data. There was barely a vacant seat in the auditorium for the duration of the conference and, with such intense interest in the subject, the conference must surely be judged both timely and successful.

Literature Cited

Cronquist, A. 1987. A botanical critique of cladism. Bot. Rev. (Lancaster) 53: 1–52.

———. 1990. Present achievements and future trends in systematics. Giorn. Bot. Ital. 124: 8 [abstract].

Kenrick, P. Alternation of generations in land plants: New phylogenetic and paleobotanical evidence. Biological Reviews (in press).

——— & P. R. Crane. 1991. Water-conducting cells in early fossil land plants: Implications for the early evolution of tracheophytes. Bot. Gaz. (Crawfordsville) 152: 335–356.

Parenti, L. 1980. A phylogenetic analysis of the land plants. Biol. J. Linn. Soc. 13: 225–242.

Sogin, M. L. 1991. Early evolution and the origin of eukaryotes. Current Opinion in Genetics and Development 1: 457–463.

Young, D. A. & P. M. Richardson. 1982. A phylogenetic analysis of extant seed plants: The need to utilize homologous characters. Taxon 31: 250–254.

PROGRESS AND PROSPECTS IN RECONSTRUCTING PLANT PHYLOGENY[1]

Michael J. Donoghue[2]

ABSTRACT

Phylogeny reconstruction has become respectable science over the last few decades, and trees are accumulating rapidly in the literature. Botanists have been active in this effort and can already cite success stories (e.g., recognition of streptophytes, stomatophytes, anthophytes, eudicots). Nevertheless, only a small number of problems have been addressed and some of these have resisted solution. To solve the toughest problems, especially those involving ancient, rapid radiations, various sources of data will need to be combined, including evidence from fossils. Furthermore, in view of limitations in analyzing data sets with many taxa, more attention must be paid to the consequences of different taxon sampling strategies and to how large, variable taxa can be represented in more inclusive studies.

Over the next few years we should continue to move toward a phylogenetic system (monophyletic groups defined by ancestry, diagnosed by characters), which will entail the elimination of familiar paraphyletic taxa. We can expect increased use of phylogenies by ecologists, molecular biologists, and others, which will force us to attend to the issue of the reliability of phylogenetic hypotheses, and will necessitate the development of a database of phylogenetic studies. Interactions with population biologists promise to be especially productive, since there are obvious mutual concerns centered on the analysis of gene trees and reticulation.

Over twenty-five years have elapsed since the publication of Willi Hennig's *Phylogenetic Systematics* (Hennig, 1966), and for well over a decade botanical systematists have been conducting numerical phylogenetic analyses. The focus of the Missouri Botanical Garden's Annual Systematics Symposium on the "Origin and Relationships of the Major Plant Groups" suggests that progress has been made, and the meeting itself documented significant advances in our understanding of several of the most challenging phylogenetic questions. The aim of this paper is to take stock, in general terms, of where things stand. Has phylogenetic analysis had a substantial impact on our understanding of plant phylogeny, and where do we go from here?

PROGRESS

Although many of the ideas underlying phylogenetic analysis have a rather long history (see Craw, 1992; Donoghue & Kadereit, 1992), phylogeny reconstruction has become respectable science only over the last few decades. This happy circumstance can be traced to a series of developments in the logic of phylogeny reconstruction (e.g., Hennig, 1966; Farris, 1983; see Sober, 1988; Swofford & Olsen, 1990), to the availability of computers and algorithms to implement this logic (e.g., Farris, 1988; Maddison & Maddison, 1992; Swofford, 1993), and to new sources of evidence, especially molecular data (e.g., Fernholm et al., 1989; Hillis & Moritz, 1990). While it is obvious that these developments have had a significant impact on plant systematics, it is not entirely clear how best to measure the progress that has been made. There are, however, several indicators that bear consideration.

LEVEL OF ACTIVITY

One measure of progress is simply the rate of publication of phylogenetic hypotheses. Phylogenetic trees are undoubtedly accumulating in the literature, but the magnitude of the effort is difficult to assess because no one has been keeping track of such information. In a survey of 79 journals published in 1989, 1990, and 1991, we recently assembled data on 1140 articles that contained trees (Sanderson et al., 1993). This remarkable number of studies (nearly a tree a day) is surely

[1] I am grateful to Bruce Baldwin, Peter Crane, Jim Doyle, David Hillis, Toby Kellogg, David Maddison, Wayne Maddison, Dick Olmstead, Mike Sanderson, and Liz Zimmer for helpful discussion and/or access to unpublished work, as well as to Mick Richardson for inviting me to participate in the symposium. My work has been supported by the NSF (BSR-8822658), the University of Arizona, and a Mellon Foundation Fellowship from the Smithsonian Institution.

[2] Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, Massachusetts 02138, U.S.A.

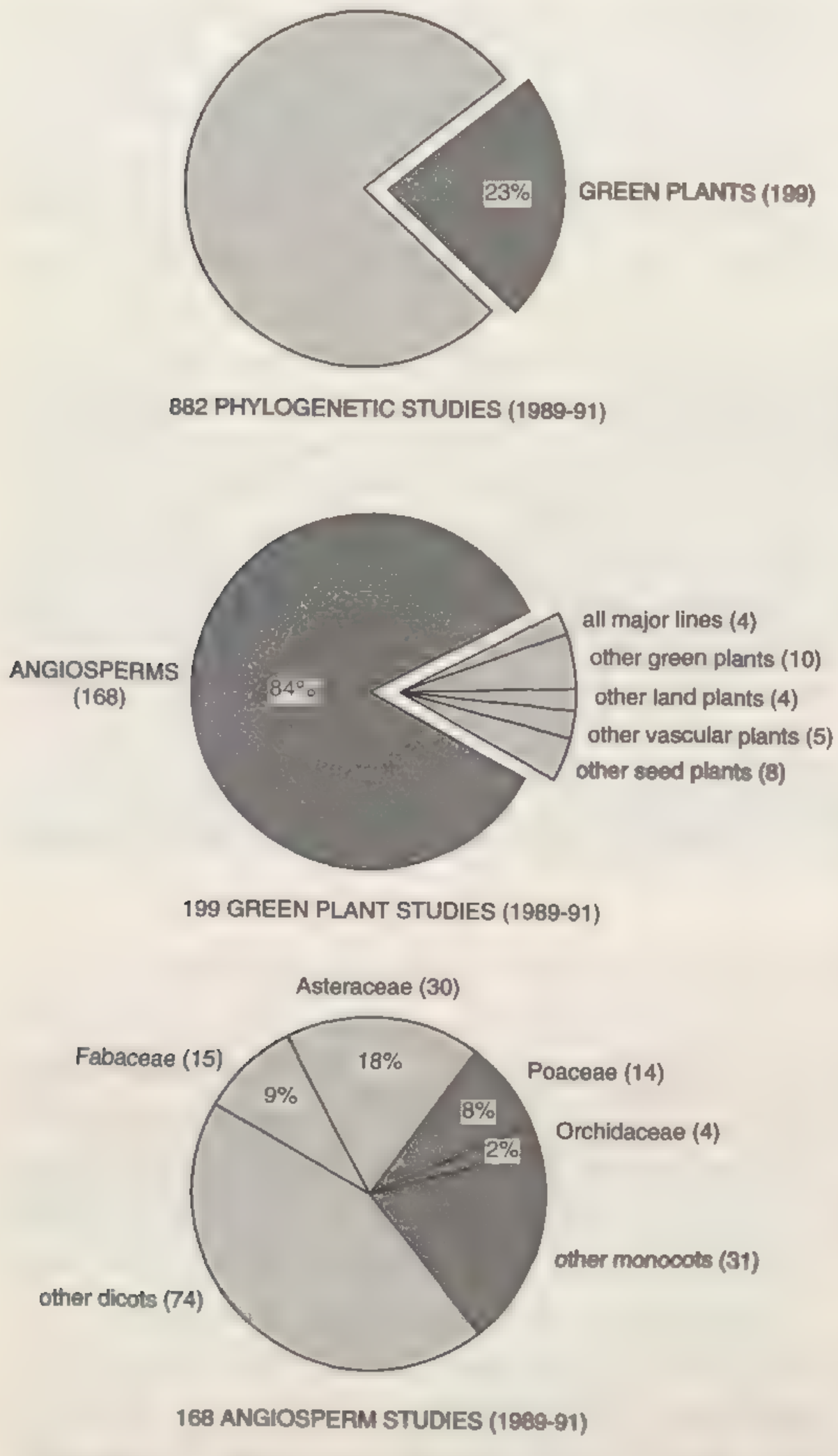

FIGURE 1. Pie charts showing aspects of the taxonomic distribution of numerical phylogenetic studies published between 1989 and 1991 (compiled from an updated version of a database assembled by Sanderson et al., 1993). Top: Studies of green plants (chlorophytes; with chlorophyll b, starch storage) account for ca. 23% of the 882 phylogenetic analyses in the Sanderson et al. database. Middle: Approximately 84% of the green plant studies are of angiosperm groups; the remainder are of "other seed plants" (specifically conifers, cycads), "other vascular plants" (ferns, lycopsids), "other embryophytes" (mosses, liverworts), "other green plants" (various "green algae"), or included representatives of "all major lines." Bottom: Of 168 angiosperm studies, 49 (ca. 29%) are of monocot groups; Asteraceae and Fabaceae account for ca. 38% of the "dicot" studies.

an underestimate inasmuch as we did not survey every journal containing phylogenetic studies and we were unable to include analyses published in books. Nevertheless, our study probably provides a reasonably accurate picture of what exists in the literature. Of the total, 882 (77%) of the studies employed some "cladistic" method (including parsimony and some distance methods, but not phenetic clustering methods such as UPGMA), and over 471 (53%) of the phylogenetic studies used some form of molecular evidence (including allozyme data), with the percentage of such studies increasing from 51% to 56% over the three-year period.

We identified 312 studies of green plant groups (ca. 27% of the total), namely organisms with chlorophyll b and starch storage, including the various lines of "green algae" and the land plants (Sanderson et al., 1993). However, 113 (36%) of these employed only phenetic techniques, a greater percentage of phenetic studies than we found in any other major group of eukaryotes. A breakdown of the remaining 199 numerical phylogenetic studies of green plants (ca. 23% of all phylogenetic studies) is shown in Figure 1. The vast majority (168, 84%) of these were of angiosperm groups. Within angiosperms, Asteraceae (30 phylogenetic studies) and Fabaceae (15 studies) received the most attention, while other large families, such as Orchidaceae (4 studies) are underrepresented. The 49 studies of monocots account for around 29% of all angiosperm studies, with 14 of these within grasses. To some extent these numbers reflect the number of species per group, but historical factors are evident as well. For example, studies of Asteraceae were stimulated by the early and promising restriction site studies of Jansen, Palmer, and colleagues (see references in Palmer et al., 1988; Jansen et al., 1992).

Figure 1 also shows that some groups have received relatively little attention, especially considering their importance in understanding phylogenetic relationships among major lines of green plants. For example, we found only five phylogenetic analyses of vascular plants other than seed plants during the three-year period, despite their great phylogenetic significance and the evident interest of pteridologists in phylogenetic questions (e.g., Wagner, 1980). Such studies, including fossil groups (e.g., "Cladoxylales," "Coenopteridales," and "progymnosperms"), are desperately needed in order to establish, for example, whether eusporangiate fern groups are more closely related to leptosporangiate ferns or perhaps to progymnosperm groups (and hence seed plants). Fortunately, zosterophylls and lycophytes (including fossils) are now receiving more attention (e.g., Bateman et al., 1992; Gensel, 1992).

Although the absolute number of molecular studies of green plant phylogeny increased slightly each year, the percentage of such studies over the three-year period fluctuated around 50%, the rest being based on morphology and/or secondary chemistry. Overall, about half of the molecular studies were

based on restriction fragment variation, especially in chloroplast DNA. The number of plant studies based on nucleotide sequences has risen dramatically since 1991 (e.g., studies of the chloroplast gene *rbc*L), and will undoubtedly continue to increase in number, but rather few such studies (32, 24% of the plant molecular studies) were published in the 1989–1991 period. Over half of the sequence studies involved ribosomal genes (see Zimmer et al., 1989; Hamby & Zimmer, 1992; Waters et al., 1992), and in the near future, especially at lower taxonomic levels, analyses of the internal transcribed spacer (ITS) regions (e.g., Baldwin, 1992; Wojciechowski et al., 1993) promise to be productive. Phylogenetic studies using "single-copy" nuclear genes are still rare, but technical difficulties in obtaining such sequences have been largely overcome, and I expect that they will play an increasingly important role.

Phylogenetic studies that include fossils are still rare, despite their potential significance (Donoghue et al., 1989). While molecular studies of fossils are promising (e.g., Golenberg et al., 1990; Soltis et al., 1992), their impact will depend on developing the ability to repeatably obtain significant segments of DNA from plant parts fossilized in standard ways.

SUCCESS STORIES

While it is obvious that botanists have actively engaged in phylogenetic research, it is more difficult to determine how successful these efforts have been. However, in several cases significant progress does appear to have been made. Some of these successes are highlighted in the accompanying symposium papers, so only a few are noted here (Fig. 2).

The studies by Mishler and colleagues (see Mishler et al., 1994, this issue) have confirmed earlier indications that green algal groups with phragmoplasts, especially charophytes such as *Coleochaete*, are more closely related to land plants than they are to other "green algae." They also solidify the view that "bryophytes" are paraphyletic, with mosses more closely related to tracheophytes. These hypotheses are being borne out by molecular evidence (Mishler et al., 1992, 1994).

Kenrick & Crane (1991) have made great progress in establishing relationships among early lines of vascular plants, suggesting that several major splitting events and morphological innovations predated the radiation giving rise to extant groups. Their detailed studies of tracheids, coupled with the remarkable discoveries of Remy and colleagues on gametophyte morphology (e.g., Remy, 1982; references in Kenrick & Crane, 1991), provide excellent examples of the importance of fossils in understanding the early evolution of vascular plants. Again, these conclusions are consistent with recent molecular evidence (e.g., Palmer et al., 1988; Manhart & Palmer, 1990; Raubeson & Jansen, 1992).

Morphological phylogenetic analyses of seed plants (Crane, 1985, 1988; Doyle & Donoghue, 1986, 1992; Loconte & Stevenson, 1990; Doyle et al., 1994, this issue; Nixon et al., 1994, this issue), while not agreeing in detail, have consistently concluded that Gnetales are the living group most closely related to angiosperms (Fig. 2). This clade is also supported (though not very strongly) by chloroplast and ribosomal sequence data (Chase et al., 1993; Hamby & Zimmer, 1992; but see Troitsky et al., 1991; Hasebe et al., 1992). An "anthophyte" clade, consisting of these two living groups plus Bennettitales and *Pentoxylon*, is a regular feature of the studies that have included fossils. Furthermore, with the exception of some analyses by Nixon et al. (1994), all of these studies have determined that Gnetales are monophyletic, with *Gnetum* and *Welwitschia* more closely related to one another than either is to *Ephedra*. In this case, the molecular data are especially compelling (Doyle et al., 1994).

There has also been consensus on the monophyly of angiosperms, a significant conclusion in view of lingering adherence to the belief that they are polyphyletic (e.g., Krassilov, 1991). Within angiosperms there have also been promising results. Perhaps most importantly, the "tricolpate" clade of Donoghue & Doyle (1989; "eudicots" of Doyle & Hotton, 1991) has surfaced in recent *rbc*L studies (Olmstead et al., 1992; Chase et al., 1993), implying that the vast majority of "dicots" (the "higher" subclasses of Cronquist, 1988; Takhtajan, 1987) form a clade, as opposed to having several separate origins among "magnoliids," as suggested previously. Further analyses are needed to check the robustness of this conclusion.

Even from this short list it is clear that "success" has not been tied to the use of any one type of evidence. In fact, the very impression of success stems from "making sense" of all of the data, including information on fossil and Recent organisms, morphology and molecules. In stressing this "criterion of veracity," Hennig (1966) provided a characteristically convincing analogy, which I have reproduced in Figure 3. In this example, the process of accounting for all of the evidence is likened to a geographer attempting to assemble the torn pieces of a map so as to bring together all of the

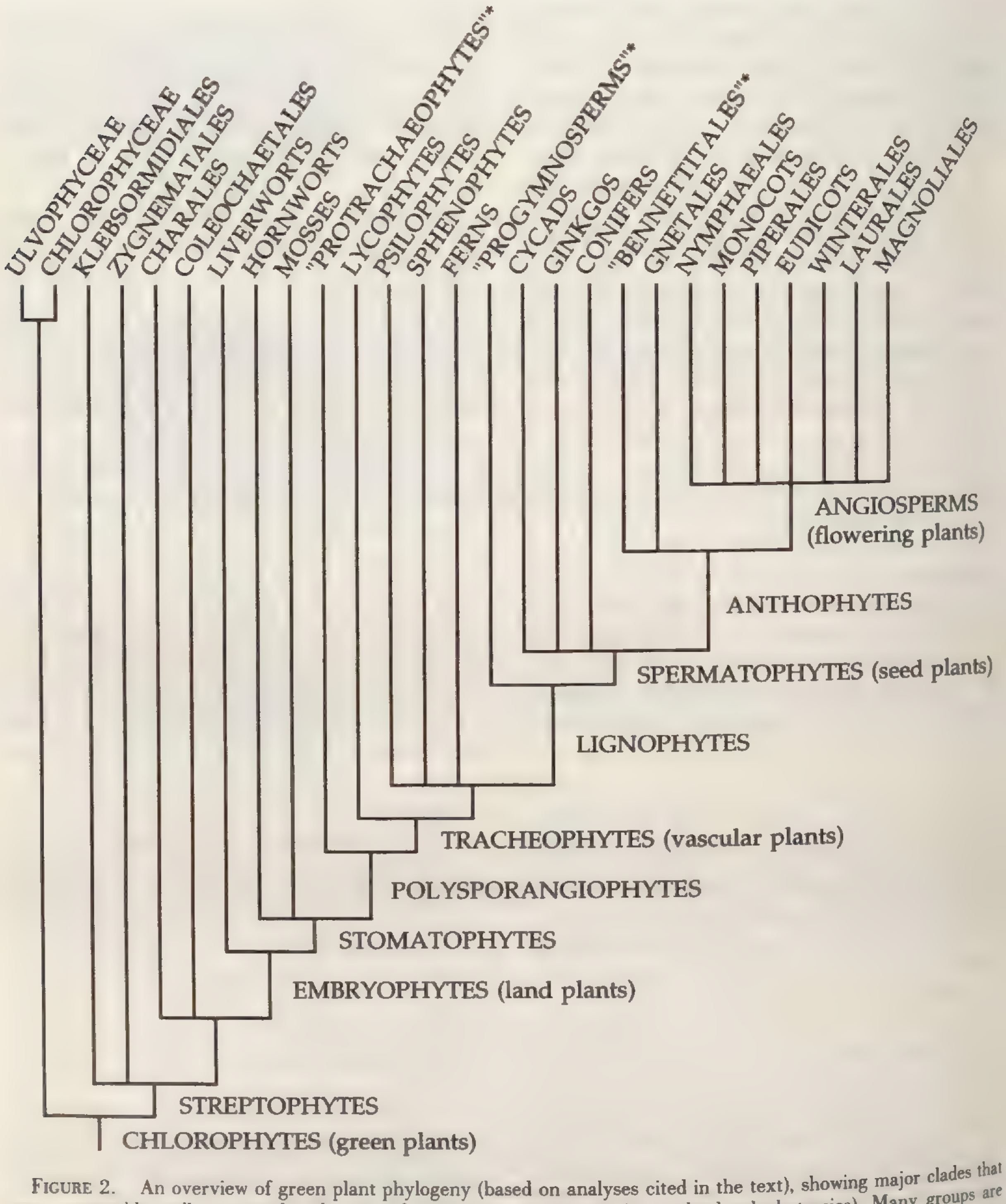

FIGURE 2. An overview of green plant phylogeny (based on analyses cited in the text), showing major clades that seem reasonably well supported and areas of continuing uncertainty (unresolved polychotomies). Many groups are omitted, and resolution is simplified to highlight familiar clades (see O'Hara, 1992). Only three fossil groups are included (marked by *), which are probably paraphyletic (quotation marks). Some of the best supported branches have long been recognized (e.g., land plants, seed plants, flowering plants), though these have not been universally accepted; others have been re-circumscribed (e.g., tracheophytes) or named (e.g., polysporangiophytes) only recently (Kenrick & Crane, 1991); several others have not yet been named (e.g., Charales+Choleochaetales+Embryophytes). Recognition of the monophyly of a number of terminal taxa (e.g., eudicots) is also an outcome of recent phylogenetic studies. Note that some traditional groups (e.g., "green algae," "bryophytes," "gymnosperms") are not monophyletic, and are not shown.

roads, rivers, and other landmarks. The corresponding operation in phylogenetic systematics is assessing, as Hennig (1966: 130) put it, "whether the differently determined views concerning the phylogenetic relationships of different groups of organisms are in agreement." Satisfaction is achieved when the pieces are assembled so that everything fits. One of the central points of the example is that a perfectly consistent explanation for any one road, or bit of evidence, might turn out to be highly unparsimonious when other features, however minor they may have seemed at the outset, are taken into consideration.

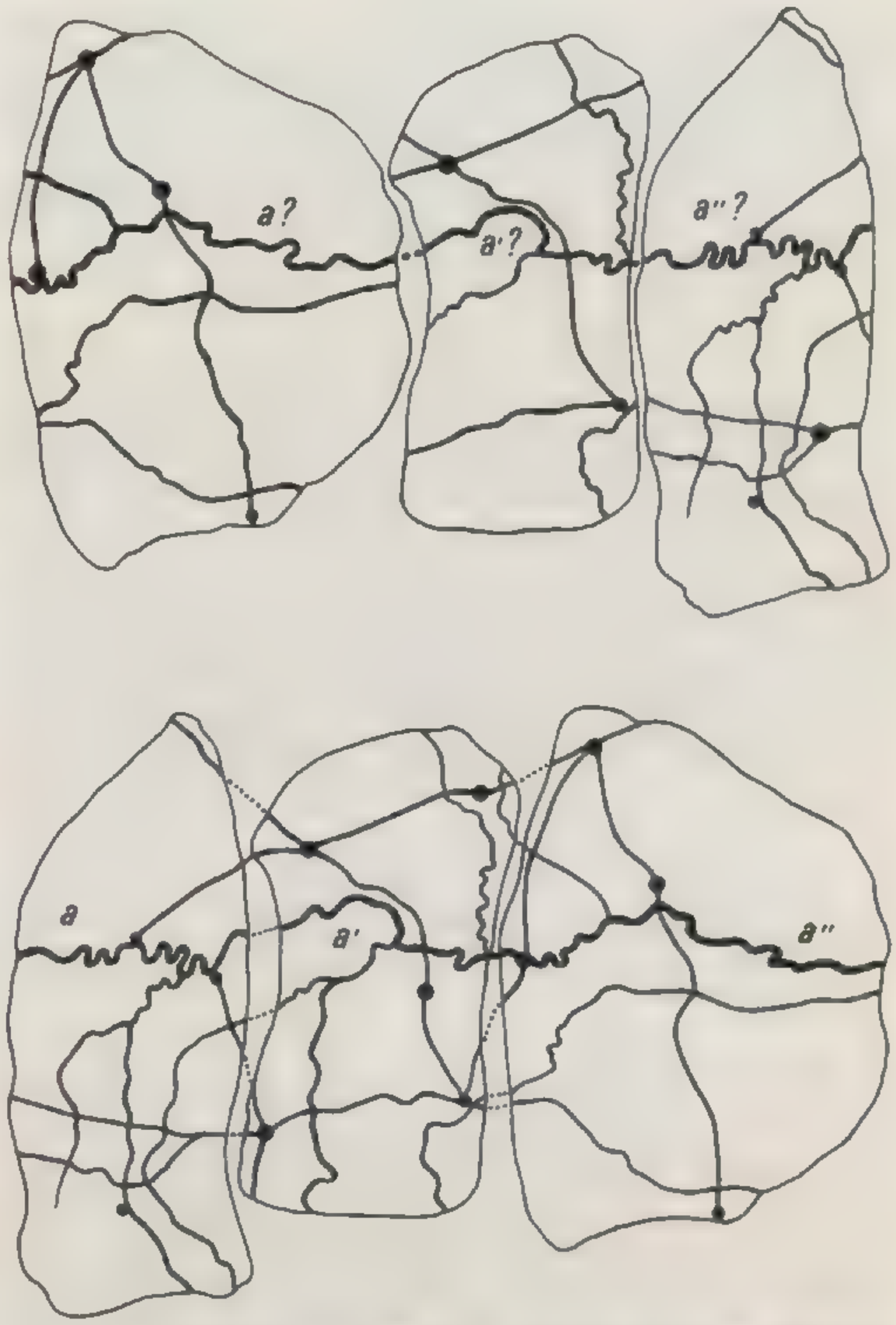

FIGURE 3. Figures 37 (top panel) and 38 (bottom panel) from Hennig (1966), illustrating the "criterion of veracity." Hennig's original captions are as follows: "Figure 37. Criterion of veracity. In the reconstruction of a topographic map from several fragments, a, a', and a" could be interpreted as adjacent sections of a stream course. The remaining elements of the map, however, remain isolated. The joining of the map fragments is wrong." "Figure 38. Criterion of veracity. If in the reconstruction of a topographic map from several fragments, a, a', and a" are interpreted as adjacent sections of a stream, the other elements of the map also join to form a sensible illustration. The joining of the map fragments is correct."

OUTSTANDING PHYLOGENETIC PROBLEMS

For each success story there are, of course, many other problems that have not been addressed or for which a satisfying result has not yet been obtained. Thus, as also shown in Figure 2, relationships among the major extant lines of seed plants (cycads, ginkgos, conifers, anthophytes) have not yet been convincingly resolved (Doyle & Donoghue, 1992; Doyle et al., 1994). Likewise, the position of the root of angiosperms, whether among "magnoliids" or among "paleoherbs," has remained unsettled (but see Doyle et al., 1994). In both cases, particular data sets fail to provide convincing support for one hypothesis over another and/or there are conflicts among the results based on different data sets. Even in these cases, however, some hypotheses appear less likely to be true than others. For example, there is little evidence that the root of angiosperms is among monocots, and I find it interesting that molecular data in particular do not support rooting the tree in the vicinity of Chloranthaceae. Furthermore, it is worth noting that conflicts appear to be as significant *among* different molecular trees (contrast Martin & Dowd, 1991; Hamby & Zimmer, 1992; Chase et al., 1993), and *among* different morphological results (contrast Dahlgren & Bremer, 1985; Donoghue & Doyle, 1989; Loconte & Stevenson, 1991; Taylor & Hickey, 1992; Nixon et al., 1994), as they are *between* molecular and morphological results.

What can be done to solve such problems? First, we can hope to obtain more decisive data. New molecular evidence will certainly be forthcoming, and traditional sources of evidence are far from being exhausted. Much of the information present in standard compendia (e.g., Cronquist, 1981) has not yet been incorporated in phylogenetic analyses. This can and should be done, but will require a critical reassessment of homology hypotheses (Donoghue & Sanderson, 1994). Furthermore, new approaches to morphology, such as detailed studies of flower development and function (e.g., Endress, 1987; Tucker, 1988; Erbar, 1991; Williams et al., 1993), continue to provide valuable phylogenetic characters. Comparative analyses that make use of recent findings on the molecular mechanisms underlying flower development (e.g., Coen & Meyerowitz, 1991) promise to be especially useful in elucidating the homology of the structures that have been most heavily used in morphological phylogenetic research.

Different sources of evidence also can be combined and analyzed simultaneously (Kluge, 1989; Barrett et al., 1991; Donoghue & Sanderson, 1992; but see Swofford, 1991; Bull et al., 1993; de Queiroz, 1993). Here the hope is that weak signals

present in several separate data sets might complement one another and provide a single stronger result. Obviously, this need not be the outcome, but it behooves us to explore such possibilities in particular cases. In the case of the angiosperm root, the combined analysis of Doyle et al. (1994) favors a placement among paleoherbs more convincingly than any single data set. This is not simply a matter of a larger number of molecular characters swamping out the morphological evidence, because some elements in the combined trees are more consistent with morphology. The temptation to compete molecules against morphology is simply counterproductive—combining the evidence may provide the best hope of success (Sytsma, 1990; Donoghue & Sanderson, 1992; Doyle et al., 1994).

Incorporation of fossils is likely to be critical in cases of presumed rapid radiation in the distant past (Donoghue et al., 1989; Huelsenbeck, 1991b; Novacek, 1992). Fossils might represent more faithfully those character combinations that were present closer to the splitting events of interest. Their addition could, in effect, "shorten" the lengths of branches leading to extant taxa, thereby lessening the chance of spurious connections owing to chance convergences (the "long-branch attraction" problem; Felsenstein, 1978). Already there are examples of this effect (e.g., "progymnosperms" relative to seed plants), and the addition of recent paleobotanical discoveries (e.g., Crane et al., 1989; Pedersen et al., 1991; Cornet, 1986) could have a similar effect as regards angiosperms (Doyle & Donoghue, 1993).

METHODOLOGICAL ISSUES

Solving difficult phylogenetic problems will require additional evidence, but it will also depend on basic methodological advances. Thus, both the thought of combining data sets and the possibility of long-branch attractions highlight the need for more attention to taxon sampling for phylogenetic analysis (e.g., Donoghue & Sanderson, 1992; Wheeler, 1992; Kellogg & Watson, 1993). This is especially critical in view of the significant limitations of presently available computer algorithms in handling large numbers of taxa (Swofford & Olsen, 1990; Maddison, 1991; Maddison et al., 1992; Penny et al., 1992). Although there is some comfort in the extensive sampling of angiosperms in the Chase et al. (1993) analysis of 499 *rbc*L sequences, the results are correspondingly difficult to interpret. It is unclear whether all (or even any) of the most parsimonious trees actually have been recovered, and it is practically impossible to evaluate alternative hypotheses critically or to explore the robustness of the results using tests such as the bootstrap (Felsenstein, 1985; Sanderson, 1989) or decay analysis (Bremer, 1988; Donoghue et al., 1992). Of course, the same limitations apply to large morphological studies (e.g., Hufford, 1992; Kellogg & Watson, 1993).

In view of these problems, analyses involving large numbers of taxa must employ carefully designed (and explicit) search strategies to discover separate "islands" of parsimonious trees (Maddison, 1991; Maddison et al., 1992; Page, 1993b; Olmstead et al., 1993). Alternatively, there may be ways of reducing the number of taxa without sacrificing accuracy. One possibility, the use of a single "exemplar" species to represent a large clade, has the advantage of avoiding (at least partially) the problem of inferring basal states for the group in question. This strategy, however, entails its own risks. Most importantly, the inadvertent choice of an exemplar that is, in reality, nested well within the clade in question, might result in a mistaken estimate of the true relationships of the group. This could happen, for example, if the exemplar belonged to one specialized line within the group, which happened to have converged on another terminal taxon in the analysis.

A second option is the use of a "placeholder" for a number of terminal taxa, where there is evidence at the outset that these form a clade. In this case, some prior information on relationships within the group may make it possible to establish a set of ancestral conditions, by finding the most parsimonious character states at the basal node of the clade in question (algorithms are described by Swofford & Maddison, 1987). This approach, advocated by Mishler (1994) under the name "compartmentalization," has been used in morphological analyses for some time (though not always very explicitly). For example, Donoghue & Doyle (1989) performed a preliminary phylogenetic analysis within a presumably monophyletic core-Laurales clade and used the results to assign states to a placeholder for that line. Similarly, Doyle et al. (1994) used preliminary hypotheses on relationships within such groups as monocotyledons to "boil down" information on a set of observed terminal taxa to a set of ancestral state assignments. Fortunately, it may be sufficient to have only a partial prior hypothesis of relationships, as the states of taxa nested well within the clade in question may be effectively "screened-off" from having any effect on the assessment of basal conditions (Maddison et al., 1984).

The use of placeholders will mean that more

than one character state will occur in some terminal taxa. An alternative approach, advocated by Nixon & Davis (1991), is always to subdivide polymorphic taxa into monomorphic terminal units. This, of course, can only aggravate the real-world problems posed by large numbers of taxa. Furthermore, subdivision based on the states of a character (one of which is presumably ancestral within the group) will result in para- or polyphyletic terminal units in many cases. For example, if angiosperms were subdivided into two terminal taxa based on the presence and absence of vessels it is highly likely that neither would be a clade. The same would be true of many other characters, such as the presence and absence of an active cambium, or different types of embryo sac development. Inclusion of nonmonophyletic terminal taxa in an analysis can result in erroneous conclusions about relationships and character evolution, at least if taxa are interpreted in the standard way, namely as representing real (single) branches of a phylogenetic tree.

In the end, the best method of coding large polymorphic taxa will depend on the circumstances. Sometimes it will be feasible and appropriate to split a polymorphic terminal unit into two or more groups (hopefully monophyletic), and this may not significantly increase the overall number of taxa. In other cases some form of compartmentalization will be possible, leaning cautiously on the results of previous analyses. The latter requires that the assumptions used in one analysis be vigorously tested in other, independent analyses, but such tests are certainly possible (e.g., Doyle et al., 1994). Another option is to simply code a terminal taxon as polymorphic, as can be done in PAUP (Swofford, 1993) and MacClade (Maddison & Maddison, 1992). In the case of multistate characters (such as nucleotides at a particular site) this need not be equivalent to coding the taxon as completely "unknown," since particular subsets of states can be specified. Although coding a taxon as unknown can sometimes have undesirable effects (Doyle & Donoghue, 1986; Nixon & Davis, 1991; Platnick et al., 1991), it may be necessary, especially to incorporate incomplete fossils (Maddison & Maddison, 1992).

Even in cases that continue to resist resolution, progress is made when relevant data and analyses are published, because, if nothing else, this clarifies the implications of alternative hypotheses. This is true, of course, only to the extent that sources of information (especially voucher specimens) are carefully documented, and only if the assumptions underlying the delimitation of taxa and characters are clearly spelled out. Phylogenetic research can be of lasting value only if all of the evidence underlying the results is made available for scrutiny. Otherwise, it is impossible to make reasoned choices among alternative hypotheses, or to learn anything at all from experience.

Prospects

What can we look forward to over the next few years? Here I will briefly highlight what I believe to be several important trends and their likely consequences. At the base of each of these trends is a more fundamental shift to what O'Hara (1988) has called "tree-thinking": understanding diversity as the product of an underlying branching process, and observed differences as having resulted from evolutionary changes along the branches of a tree. That the shift away from a linear view of evolution is far from complete is evidenced by the language still so often used to describe evolutionary history, such as "lower" and "higher" in reference to taxa (O'Hara, 1992). Fortunately, however, tree-thinking is likely to figure more prominently in the curriculum, with software such as MacClade (Maddison & Maddison, 1992) making it easy and fun to explore the implications of evolutionary trees.

A phylogenetic system

Although major changes will undoubtedly take time, I suspect that botanists will continue to move toward a truly phylogenetic system. By this I mean that taxa will be delimited so as to conform to our best estimates of phylogeny and will be defined in terms of ancestry rather than in terms of the characters used to diagnose them (Hennig, 1966; de Queiroz, 1988, 1992; Donoghue & Cantino, 1988; de Queiroz & Gauthier, 1992). In practical terms this will mean eliminating some familiar paraphyletic groups. An excellent example is provided by phylogenetic research on Asteraceae, culminating recently (Bremer et al., 1992) in several new names to reflect conclusions that are well supported by different sources of evidence (e.g., Barnadesioideae as the sister group of the rest of the family).

Many more changes of this sort will be made as our understanding of phylogeny improves. In particular, it is clear that some traditional angiosperm families are paraphyletic, with one or more monophyletic families nested within them. For example, Cantino (1992) has carefully documented the origin of several lines of Lamiaceae from within Verbenaceae. Judd et al. (1994) have documented similar situations in phylogenetic analyses of other presumably closely related families. In particular, Asclepiadaceae appear to be nested within a para-

phyletic Apocynaceae, Apiaceae within Araliaceae, Brassicaceae within Capparaceae, Valerianaceae plus Dipsacaceae within Caprifoliaceae, Urticaceae within Moraceae, and Aceraceae and Hippocastanaceae within Sapindaceae. Many of these conclusions based on morphology are now also supported by molecular evidence (e.g., Chase et al., 1993). In most of these cases, we have proposed to eliminate paraphyly through recognition of a single more inclusive family (Judd et al., 1994). This, we hope, will help counteract a bias on the part of temperate botanists to segregate and elevate the rank of mainly temperate, mainly herbaceous groups, leaving behind a residue of woody tropical plants with which they are less familiar.

Although the shift to monophyly may entail rather major changes in some cases, this should hardly be viewed with dismay. Instead, such changes are a concrete sign that we are making progress in understanding phylogeny. Furthermore, although there will be resistance to changing traditional names, such changes are very likely to occur in the long run because a phylogenetic system is most useful in helping us understand evolutionary and ecological processes, biogeography, and so on (Hennig, 1966). Moreover, recognition of monophyletic groups makes it much easier to teach plant diversity and for students to learn about it. It also helps from the standpoint of continued analysis of phylogeny to have names for the clades we work with. The name "anthophyte," for example, has been useful in describing seed plant phylogeny. Likewise, we hope that the "stem-based" name "angiophyte" (Doyle & Donoghue, 1993) will facilitate discussion of how fossils such as *Sanmiguelia* (Cornet, 1986) relate to modern angiosperms.

In addition to better phylogenies, the development of a phylogenetic system requires attention to the logic of phylogenetic taxonomy and nomenclatural conventions. Here the analysis and recommendations of de Queiroz & Gauthier (1992) provide an excellent starting point. Among other things, I agree with them that we should seriously reconsider the need to designate standard Linnean ranks, especially in view of the evident temptation to treat taxa assigned to the same taxonomic rank as though they are somehow equivalent. Such rank-based approaches can lead, for instance, to systematic errors in studies of rates of extinction and diversification (Doyle & Donoghue, 1993).

PHYLOGENIES IN USE

The use of phylogenies by ecologists, paleontologists, biogeographers, molecular biologists, conservationists, and others will surely continue to increase (e.g., Brooks & McLennan, 1991; Harvey & Pagel, 1991). In the case of angiosperms, for example, the availability of trees has already had an impact on studies of a wide variety of characters, including vessels (Young, 1981; Donoghue & Doyle, 1989), dioecy (Donoghue, 1989), double fertilization and endosperm (Donoghue, 1989; Freidman, 1992; Donoghue & Scheiner, 1992), pollen morphology (Doyle & Hotton, 1991), pollination (Pellmyr, 1992), and self-incompatibility (Weller et al., 1994). Many other ideas on the direction of morphological evolution (discussed, for example, by Stebbins, 1974; Carlquist, 1975; Cronquist, 1988; Takhtajan, 1991) will soon be tested in a phylogenetic context. Similarly, phylogenies will have an increasing impact on our understanding of molecular evolution. For instance, we can look forward to a fruitful period of "reciprocal illumination" between studies of plant phylogeny and molecular genetic analyses of the mechanisms underlying flower development (Coen & Meyerowitz, 1991).

The use of phylogenies in other studies will force phylogenetic systematists to attend to the issue of reliability. Quite naturally, those who intend to rely on phylogenies will want some indication as to how believable they are. A variety of methods have been developed (e.g., Felsenstein, 1985; Bremer, 1988; Sanderson, 1989; Archie, 1989; Hillis, 1991; Huelsenbeck, 1991a; Goloboff, 1991a; Faith, 1991; Donoghue et al., 1992) and there is a growing (mostly critical) literature on the logic and behavior of such methods (e.g., Carpenter, 1992; Goloboff, 1991b; Kallersjo et al., 1992; Hillis & Bull, 1993). Here it will be critical to develop a deeper understanding of the underlying philosophical and statistical issues. If it emerges that particular methods are unsatisfactory, then it behooves us to articulate exactly why this is the case and then to develop and test better methods. In the meantime, users of trees should be warned of uncertainties and encouraged to take into account ambiguities in estimates of the phylogeny and of character change (e.g., Maddison, 1991; Maddison et al., 1992; Weller et al., in press).

Progress in assessing confidence will require a better understanding of possible sources of error, such as long-branch attraction (e.g., Albert et al., 1994). In particular, we need to know more precisely how to distinguish real signal from spurious results. Despite their limitations (Hillis et al., 1992), computer simulations will continue to be a useful approach to such questions, making it possible to explore a very wide range of possible parameter values (e.g., Lanyon, 1988; Huelsenbeck & Hillis, 1993; Kim et al., 1993). Of course, such studies

leave open the critical question of exactly where in parameter space any particular problem is situated, but it is nevertheless important to formalize the universe of possibilities and the impact of critical variables.

Work with known phylogenies (e.g., Atchley & Fitch, 1991; Hillis et al., 1992) and experimentation with real data sets (e.g., Smith, 1989; Donoghue et al., 1989; Allard & Miyamoto, 1992) also will be useful. An approach that deserves more attention is the use of random nucleotide sequences as benchmarks to help determine whether real sequences have retained signal relative to a particular phylogenetic problem (e.g., Miyamoto and Boyle, 1989; Wheeler, 1990; Maddison et al., 1992). For example, David Maddison and I (unpublished analysis) are using this approach to evaluate the attachment of real outgroup sequences to the *Ceratophyllum* branch in angiosperm trees based on *rbc*L data (Les et al., 1991; Chase et al., 1993). Is this the true position of the root, or are real outgroup sequences so highly diverged that, in effect, they no longer retain phylogenetic information? Our preliminary studies show that most "random" sequences (generated under several models) also attach to the "long" *Ceratophyllum* branch. Nevertheless, there are some aspects of the behavior of real outgroup sequences that deviate from any of the random sequences we have investigated, implying that the real sequences may not be entirely devoid of phylogenetic signal. More experiments are needed, as are more sensitive statistical tests.

Increased interest in phylogenies also demands that we develop better ways of making information about them accessible to potential users. We need, in short, to assemble a database of phylogenetic data and trees (Sanderson et al., 1993). At the same time, we should establish standard means for depositing phylogenetic data as a co-requisite of publication, just as nucleotide sequences are now routinely transmitted electronically to repositories such as Genbank (Cinkosky et al., 1991). On a practical level, such a database would allow systematists to respond rapidly to requests for phylogenetic information in connection, for example, with conservation efforts (e.g., Vane-Wright et al., 1991). Moreover, accessibility of the full range of phylogenetic studies surely would facilitate the search for general patterns; for example, patterns in levels of homoplasy (e.g., Sanderson & Donoghue, 1989), or in tree shape (e.g., Savage, 1983; Guyer & Slowinski, 1991, 1993). It would also revolutionize the search for general patterns in geographic distributions, by allowing (at least potentially) ready access to every tree with taxa present in particular areas of endemism (e.g., Nelson & Platnick, 1981; Page, 1991).

PHYLOGENIES AND POPULATION BIOLOGY

Systematics is sometimes portrayed as being neatly separated from population biology, and it is sometimes implied that this gap should be maintained (e.g., Nixon & Wheeler, 1990). This, I believe, is a mistake. On the contrary, interactions with population biologists should be promoted actively. Such contacts promise to be especially fruitful in view of obvious mutual concerns centered on the analysis of gene trees and the recent emergence of coalescence theory (Pamilo & Nei, 1988; Avise, 1989; Takahata, 1989; Hudson, 1990; Doyle, 1992; Page, 1993a; Baum & Shaw, in press; Maddison, in press).

The application of phylogenetic methods to what have traditionally been population-level problems is yielding promising results already. For example, Slatkin & Maddison (1990) devised a phylogenetic measure of gene flow, and Felsenstein (1992) has approached the estimation of effective population size from a phylogenetic standpoint. It is perhaps less obvious how systematists, especially those of us primarily concerned with deeper branching events, stand to benefit from interacting with population biologists. However, several fundamental questions require population-level input. One such concern is the possibility of a false estimate of phylogeny based on uniparentally inherited organellar DNA (e.g., Rieseberg & Soltis, 1991; Doyle, 1992). Whether lineage sorting, for example, is likely to have been an important factor in a particular case depends on population sizes and the time intervals between splitting events. We recognize that these are the important parameters, and we know something about their critical values, based on models developed by population geneticists (e.g., Pamilo & Nei, 1988; see Maddison, in press). Moreover, population biologists may be able to estimate these parameters in particular cases. Ultimately, this could bear directly on the way in which organellar data are integrated with other evidence in phylogenetic analysis (Doyle, 1992).

Input from population geneticists also will be critical in understanding processes such as concerted evolution and the dynamics underlying the establishment of paralogous genes, issues of obvious interest to molecular systematists (e.g., Zimmer et al., 1980; Patterson, 1988; Sanderson & Doyle, 1992). Better understanding of these phenomena will help guard against mistaken comparisons, and will allow us to turn them to our advantage in some cases. For example, comparison of phylogenies

based on paralogous genes may make it possible to establish the root of a tree. In fact, this approach allowed Iwabe et al. (1989) to root the tree of life, despite the lack of obvious outgroups.

The ability to compare trees based on both nuclear and organellar genes obviously has expanded our ability to identify hybrids and specify their parentage (e.g., Soltis et al., 1989; Rieseberg & Brunsfeld, 1992). Although hybrids have occasionally been discussed by phylogeneticists (papers in Platnick & Funk, 1983; Funk, 1985), detailed empirical studies of their impact on phylogeny reconstruction have appeared only recently (McDade, 1992). Nevertheless, botanists should soon play a major role in developing methods for the recognition and incorporation of reticulations in phylogenetic analysis (e.g., Rieseberg & Morefield, in press). Ultimately, what is needed is a general theory covering reticulations of all sorts (Page, 1993a), including recombination in the case of genes (Hein, 1990), lateral transfer of DNA (Valdez & Piñero, 1992), and even the fusion of entire biotas in biogeography (Cracraft, 1988). The development of such a theory depends on breaking down whatever barriers have tended to separate population biologists from systematists.

Summary

It seems clear that headway has been made in understanding plant phylogeny over the last few decades, and there is every reason to expect continued success. It is also clear, however, that many basic phylogenetic questions will be rather difficult to answer. New morphological and molecular evidence, in combination with the old, should eventually point the way to a solution. At the same time, methodological advances will allow us to get more mileage out of whatever data are available.

Better phylogenies will lead (hopefully) to taxonomic changes, and will surely encourage the use of trees outside of systematics. One result will be increased attention to problems of taxon sampling and to methods for assessing the reliability of phylogenetic hypotheses. Eventually, we will see the development of an even more comprehensive phylogenetic theory, incorporating reticulation of all kinds and transcending the boundaries of traditional disciplines.

Literature Cited

Albert, V. A., A. Backlund, K. Bremer, M. W. Chase, J. R. Manhart, B. D. Mishler & K. C. Nixon. 1994. Functional constraints and *rbc*L evidence for land plant phylogeny. Ann. Missouri Bot. Gard. 81: 534–567.

Allard, M. W. & M. M. Miyamoto. 1992. Perspective: Testing phylogenetic approaches with empirical data, as illustrated with the parsimony method. Molec. Biol. Evol. 9: 778–786.

Archie, J. W. 1989. A randomization test for phylogenetic information in systematic data. Syst. Zool. 38: 239–252.

Atchley, W. R. & W. M. Fitch. 1991. Gene trees and the origin of inbred strains of mice. Science 254: 554–558.

Avise, J. C. 1989. Gene trees and organismal histories: A phylogenetic approach to population biology. Evolution 43: 1192–1208.

Baldwin, B. G. 1992. Phylogenetic utility of the internal transcribed spacers of nuclear ribosomal DNA in plants: An example from the Compositae. Molecular Phylogenetics and Evolution 1: 3–16.

Barrett, M., M. J. Donoghue & E. Sober. 1991. Against consensus. Syst. Zool. 40: 486–493.

Bateman, R. M., W. A. DiMichele & D. A. Willard. 1992. Experimental cladistic analysis of anatomically preserved arborescent lycopsids from the Carboniferous of Euramerica: An essay on paleobotanical phylogenetics. Ann. Missouri Bot. Gard. 79: 500–559.

Baum, D. A. & K. L. Shaw. The genealogical species. *In* P. C. Hoch & A. G. Stephenson (editors), Experimental and Molecular Approaches to Plant Biosystematics. Monogr. Syst. Bot. Missouri Bot. Gard. (in press).

Bremer, K. 1988. The limits of amino acid sequence data in angiosperm phylogenetic reconstruction. Evolution 42: 795–803.

———, R. K. Jansen, P. O. Karis, M. Kallersjo, S. C. Keeley, K.-J. Kim, H. J. Michaels, J. D. Palmer & R. S. Wallace. 1992. A review of the phylogeny and classification of the Asteraceae. Nordic J. Bot. 12: 141 148.

Brooks, D. R. & D. A. McLennan. 1991. Phylogeny, Ecology, and Behavior. Univ. Chicago Press, Chicago.

Bull, J. J., J. P. Huelsenbeck, C. W. Cunningham, D. L. Swofford & P. J. Waddell. 1993. Partitioning and combining data in phylogenetic analysis. Syst. Biol. 42: 384–397.

Cantino, P. D. 1992. Evidence for a polyphyletic origin of the Labiatae. Ann. Missouri Bot. Gard. 79: 361–379.

Carlquist, S. 1975. Ecological Strategies of Xylem Evolution. Univ. California Press, Berkeley, California.

Carpenter, J. M. 1992. Random cladistics. Cladistics 8: 147–153.

Chase, M. W., et al. (41 others). 1993. Phylogenetics of seed plants: An analysis of nucleotide sequences from the plastid gene *rbc*L. Ann. Missouri Bot. Gard. 80: 528–580.

Cinkosky, M. J., J. W. Fickett, P. Glina & C. Burks. 1991. Electronic data publishing and GenBank. Science 252: 1273–1277.

Coen, E. S. & E. M. Meyerowitz. 1991. The war of the whorls: Genetic interactions controlling flower development. Nature 353: 31–37.

Cornet, B. 1986. The leaf venation and reproductive structures of a Late Triassic angiosperm, *Sanmiguelia lewissi*. Evol. Theory 7: 231–309.

Cracraft, J. 1988. Deep-history biogeography: Re-

trieving the historical pattern of evolving continental biotas. Syst. Zool. 37: 221–236.

CRANE, P. R. 1985. Phylogenetic analysis of seed plants and the origin of angiosperms. Ann. Missouri Bot. Gard. 72: 716–793.

———. 1988. Major clades and relationships in the "higher" gymnosperms. Pp. 218–272 *in* C. B. Beck (editor), Origin and Evolution of Gymnosperms. Columbia Univ. Press, New York.

———, E. M. FRIIS & K. R. PEDERSEN. 1989. Reproductive structure and function in Cretaceous Chloranthaceae. Pl. Syst. Evol. 165: 211–226.

CRAW, R. 1992. Margins of cladistics: Identity, difference and place in the emergence of phylogenetic systematics, 1864–1975. Pp. 65–107 *in* P. Griffiths (editor), Trees of Life. Kluwer Academic, Netherlands.

CRONQUIST, A. 1981. An Integrated System of Classification of Flowering Plants. Columbia Univ. Press, New York.

———. 1988. The Evolution and Classification of Flowering Plants. New York Bot. Gard., Bronx.

DAHLGREN, R. & K. BREMER. 1985. Major clades of angiosperms. Cladistics 1: 349–368.

DONOGHUE, M. J. 1989. Phylogenies and the analysis of evolutionary sequences, with examples from seed plants. Evolution 43: 1137–1156.

——— & P. D. CANTINO. 1988. Paraphyly, ancestors, and the goals of taxonomy: A botanical defense of cladism. Bot. Rev. 54: 107–128.

——— & J. A. DOYLE. 1989. Phylogenetic analysis of angiosperms and the relationships of Hamamelidae. Pp. 17–45 *in* P. Crane & S. Blackmore (editors), Evolution, Systematics and Fossil History of the Hamamelidae. Clarendon Press, Oxford.

——— & J. W. KADEREIT. 1992. Walter Zimmermann and the growth of phylogenetic theory. Syst. Biol. 41: 74–85.

——— & M. J. SANDERSON. 1992. The suitability of molecular and morphological evidence in reconstructing plant phylogeny. Pp. 340–368 *in* P. S. Soltis, D. E. Soltis & J. J. Doyle (editors), Molecular Systematics in Plants. Chapman & Hall, New York.

——— & ———. 1994. Complexity and homology in plants. Pp. 393–421 *in* B. Hall (editor), Homology: The Hierarchical Basis of Comparative Biology. Academic Press, San Diego.

——— & S. M. SCHEINER. 1992. The evolution of endosperm: A phylogenetic account. Pp. 356–389 *in* R. Wyatt (editor), Ecology and Evolution of Plant Reproduction: New Approaches. Chapman & Hall, New York.

———, R. G. OLMSTEAD, J. F. SMITH & J. D. PALMER. 1992. Phylogenetic relationships of Dipsacales based on *rbc*L sequences. Ann. Missouri Bot. Gard. 79: 333–345.

———, J. A. DOYLE, J. GAUTHIER, A. G. KLUGE & T. ROWE. 1989. The importance of fossils in phylogeny reconstruction. Annual Rev. Ecol. Syst. 20: 431–460.

DOYLE, J. A. & M. J. DONOGHUE. 1986. Seed plant phylogeny and the origin of angiosperms: An experimental cladistic approach. Bot. Rev. 52: 321–431.

——— & ———. 1992. Fossils and seed plant phylogeny revisited. Brittonia 44: 89–106.

——— & ———. 1993. Phylogenies and angiosperm diversification. Paleobiology 19: 141–167.

——— & C. L. HOTTON. 1991. Diversification of early angiosperm pollen in a cladistic context. Pp. 169–195 *in* S. Blackmore & S. H. Barnes (editors), Pollen and Spores. Clarendon Press, Oxford.

———, M. J. DONOGHUE & E. A. ZIMMER. 1994. Integration of morphological and ribosomal RNA data on the origin of angiosperms. Ann. Missouri Bot. Gard. 81: 419–450.

DOYLE, J. J. 1992. Gene trees and species trees: Molecular systematics as one-character taxonomy. Syst. Bot. 17: 144–163.

ENDRESS, P. K. 1987. Floral phyllotaxis and floral evolution. Bot. Jahrb. Syst. 108: 417–438.

ERBAR, C. 1991. Sympetaly—A systematic character? Bot. Jahrb. Syst. 112: 417–451.

FAITH, D. P. 1991. Cladistic permutation tests for monophyly and nonmonophyly. Syst. Zool. 40: 366–375.

FARRIS, J. S. 1983. The logical basis of phylogenetic analysis. Pp. 7–36 *in* N. I. Platnick & V. A. Funk (editors), Advances in Cladistics, vol. 2. Columbia Univ. Press, New York.

———. 1988. Hennig 86. Published by the author, Port Jefferson Station, New York.

FELSENSTEIN, J. 1978. Cases in which parsimony or compatibility methods will be positively misleading. Syst. Zool. 27: 401–410.

———. 1985. Confidence limits on phylogenies: An approach using the bootstrap. Evolution 39: 783–791.

———. 1992. Estimating effective population size from samples of sequences: Inefficiency of pairwise and segregating sites as compared to phylogenetic estimates. Genetical Research 59: 139–147.

FERNHOLM, B., K. BREMER & H. JORNVALL. 1989. The Hierarchy of Life. Molecules and Morphology in Phylogenetic Reconstruction. Elsevier, Amsterdam.

FREIDMAN, W. E. 1992. Evidence of a pre-angiosperm origin of endosperm: Implications for the evolution of flowering plants. Science 225: 336–339.

FUNK, V. A. 1985. Phylogenetic patterns and hybridization. Ann. Missouri Bot. Gard. 72: 681–715.

GENSEL, P. G. 1992. Phylogenetic relationships of the zosterophylls and lycopsids: Evidence from morphology, paleoecology, and cladistic methods of inference. Ann. Missouri Bot. Gard. 79: 450–473.

GOLENBERG, E. M., D. E. GIANNASI, M. T. CLEGG, C. J. SMILEY, M. DURBIN, D. HENDERSON & G. ZURAWSKI. 1990. Chloroplast DNA sequence from a Miocene *Magnolia* species. Nature 344: 656–658.

GOLOBOFF, P. 1991a. Homoplasy and the choice among cladograms. Cladistics 7: 215–232.

———. 1991b. Random data, homoplasy and information. Cladistics 7: 395–406.

GUYER, C. & J. B. SLOWINSKI. 1991. Comparison of observed phylogenetic topologies with null expectations among three monophyletic lineages. Evolution 45: 340–350.

——— & J. B. SLOWINSKI. 1993. Adaptive radiation and the topology of large phylogenies. Evolution 47: 253–263.

HAMBY, R. K. & E. A. ZIMMER. 1992. Ribosomal RNA as a phylogenetic tool in plant systematics. Pp. 50–91 *in* P. S. Soltis, D. E. Soltis & J. J. Doyle (editors), Molecular Systematics in Plants. Chapman and Hall, New York.

HARVEY, P. H. & M. D. PAGEL. 1991. The Comparative

Method in Evolutionary Biology. Oxford Univ. Press, Oxford.

HASEBE, M., R. KOFUJI, M. ITO, M. KATO, K. IWATSUKI & K. UEDA. 1992. Phylogeny of gymnosperms inferred from *rbc*L gene sequences. Bot. Mag. Tokyo 105: 673–679.

HEIN, J. 1990. Reconstructing evolution of sequences subject to recombination using parsimony. Math. Biosci. 98: 185–200.

HENNIG, W. 1966. Phylogenetic Systematics. Univ. Illinois Press, Urbana.

HILLIS, D. M. 1991. Discriminating between phylogenetic signal and random noise in DNA sequences. Pp. 278–294 *in* M. M. Miyamoto & J. Cracraft (editors), Phylogenetic Analysis of DNA Sequences. Oxford Univ. Press, New York.

——— & J. J. BULL. 1993. An empirical test of bootstrapping as a method for assessing confidence in phylogenetic analysis. Syst. Biol. 42: 182–192.

——— & C. MORITZ (editors). 1990. Molecular Systematics. Sinauer Assoc., Sunderland, Massachusetts.

———, J. J. BULL, M. E. WHITE, M. R. BADGETT & I. J. MOLINEUX. 1992. Experimental phylogenetics: Generation of a known phylogeny. Science 255: 589–592.

HUDSON, R. R. 1990. Gene genealogies and the coalescent process. Oxford Surv. Evol. Biol. 7: 1–44.

HUELSENBECK, J. P. 1991a. Tree-length distribution skewness: An indicator of phylogenetic information. Syst. Zool. 40: 257–270.

———. 1991b. When are fossils better than extant taxa in phylogenetic analysis? Syst. Zool. 40: 458–469.

——— & D. M. HILLIS. 1993. Success of phylogenetic methods in the four-taxon case. Syst. Biol. 42: 247–264.

HUFFORD, L. D. 1992. Rosidae and their relationships to other nonmagnoliid dicotyledons: A phylogenetic analysis using morphological and chemical data. Ann. Missouri Bot. Gard. 79: 218–248.

IWABE, N., K. KUMA, M. HASEGAWA, S. OSAWA & T. MIYATA. 1989. Evolutionary relationship of archaebacteria, eubacteria, and eukaryotes inferred from phylogenetic trees of duplicated genes. Proc. Natl. Acad. Sci. USA 86: 9355–9359.

JANSEN, R. K., H. J. MICHAELS, R. S. WALLACE, K.-J. KIM, S. KEELEY, L. WATSON & J. D. PALMER. 1992. Chloroplast DNA variation in the Asteraceae: Phylogenetic and evolutionary implications. Pp. 252–279 *in* P. S. Soltis, D. E. Soltis & J. J. Doyle (editors), Molecular Systematics of Plants. Chapman and Hall, New York.

JUDD, W. S., R. W. SANDERS & M. J. DONOGHUE. 1994. Angiosperm family pairs: Preliminary phylogenetic analyses. Harvard Papers in Botany 5: 1–51.

KALLERSJO, M., J. S. FARRIS, A. G. KLUGE & C. BULT. 1992. Skewness and permutation. Cladistics 8: 275–287.

KELLOGG, E. A. & L. WATSON. 1993. Phylogenetic studies of a large data set. I. Bambusoideae, Andropogonoideae, and Pooideae (Gramineae). Bot. Rev. 59: 273–343.

KENRICK, P. & P. R. CRANE. 1991. Water-conducting cells in early fossil land plants: Implications for the early evolution of Tracheophytes. Bot. Gaz. 152: 335–356.

KIM, J., F. J. ROHLF & R. R. SOKAL. 1993. The accuracy of phylogenetic estimation using the neighbor-joining method. Evolution 47: 471–486.

KLUGE, A. J. 1989. A concern for evidence and a phylogenetic hypothesis of relationships among *Epicrates* (Bovidae, Serpentes). Syst. Zool. 38: 7–25.

KRASSILOV, V. A. 1991. The origin of angiosperms: New and old problems. Trends Ecol. Evol. 6: 215–220.

LANYON, S. M. 1988. The stochastic mode of molecular evolution: What consequences for systematic investigations? Auk 105: 565–573.

LES, D., D. K. GARVIN & C. F. WIMPEE. 1991. Molecular evolutionary history of ancient aquatic angiosperms. Proc. Natl. Acad. Sci. USA 88: 10119–10123.

LOCONTE, H. & D. W. STEVENSON. 1990. Cladistics of the Spermatophyta. Brittonia 42: 197–211.

——— & ———. 1991. Cladistics of the Magnoliidae. Cladistics 7: 267–296.

MADDISON, D. R. 1991. The discovery and importance of multiple islands of most-parsimonious trees. Syst. Zool. 40: 315–328.

———, M. RUVOLO & D. L. SWOFFORD. 1992. Geographic origins of human mitochondrial DNA: Phylogenetic evidence from control region sequences. Syst. Biol. 41: 111–124.

MADDISON, W. P. Phylogenetic histories within and between species. *In* P. C. Hoch & A. G. Stephenson (editors), Experimental and Molecular Approaches to Plant Biosystematics. Monogr. Syst. Bot. Missouri Bot. Gard. (in press).

——— & D. R. MADDISON. 1992. MacClade: Interactive Analysis of Phylogeny and Character Evolution, Vers. 3.0. Sinauer Assoc., Sunderland, Massachusetts.

———, M. J. DONOGHUE & D. R. MADDISON. 1984. Outgroup analysis and parsimony. Syst. Zool. 33: 83–103.

MANHART, J. R. & J. D. PALMER. 1990. The gain of two chloroplast tRNA introns marks the green algal ancestor of land plants. Nature 345: 268–270.

MARTIN, P. G. & J. M. DOWD. 1991. Studies of angiosperm phylogenies using protein sequences. Ann. Missouri Bot. Gard. 78: 296–337.

MCDADE, L. A. 1992. Hybrids and phylogenetic systematics. II. The impact of hybrids on cladistic analysis. Evolution 46: 1329–1346.

MISHLER, B. D. 1994. The cladistic analysis of molecular and morphological data. Amer. J. Phys. Anthropol. (in press).

———, L. A. LEWIS, M. A. BUCHHEIM, K. S. RENZAGLIA, D. J. GARBARY, C. F. DELWICHE, F. W. ZECHMAN, T. S. KANTZ & R. L. CHAPMAN. 1994. Phylogenetic relationships of the "green algae" and "bryophytes." Ann. Missouri Bot. Gard. 81: 451–483.

———, P. H. THRALL, J. S. HOPPLE, E. DE LUNA & R. VILGALYS. 1992. A molecular approach to the phylogeny of bryophytes: Cladistic analysis of chloroplast-encoded 16S and 23S ribosomal RNA genes. Bryologist 95: 172–180.

MIYAMOTO, M. M. & S. M. BOYLE. 1989. The potential importance of mitochondrial DNA sequence data to eutherian mammal phylogeny. Pp. 437–450 *in* B. Fernholm, K. Bremer & H. Jornvall (editors), The Hierarchy of Life. Molecules and Morphology in Phylogenetic Analysis. Elsevier, Amsterdam.

NELSON, G. & N. I. PLATNICK. 1981. Systematics and Biogeography: Cladistics and Vicariance. Columbia Univ. Press, New York.

NIXON, K. C. & J. I. DAVIS. 1991. Polymorphic taxa, missing values and cladistic analysis. Cladistics 7: 233–241.

——— & Q. D. WHEELER. 1990. An amplification of the phylogenetic species concept. Cladistics 6: 211–223.

———, W. L. CREPET, D. STEVENSON & E. M. FRIIS. 1994. A reevaluation of seed plant phylogeny. Ann. Missouri Bot. Gard. 81: 484–533.

NOVACEK, M. J. 1992. Fossils as critical data for phylogeny. Pp. 46–88 *in* M. J. Novacek & Q. D. Wheeler (editors), Extinction and Phylogeny. Columbia Univ. Press, New York.

O'HARA, R. J. 1988. Homage to Clio, or, toward an historical philosophy for evolutionary biology. Syst. Zool. 37: 142–155.

———. 1992. Telling the tree: Narrative representation and the study of evolutionary history. Biol. Philos. 7: 135–160.

OLMSTEAD, R. G., B. BREMER, K. M. SCOTT & J. D. PALMER. 1993. A parsimony analysis of the Asteridae sensu lato based on *rbc*L sequences. Ann. Missouri Bot. Gard. 80: 700–722.

———, H. J. MICHAELS, K. M. SCOTT & J. D. PALMER. 1992. Monophyly of the Asteridae and identification of their major lineages inferred from DNA sequences of *rbc*L. Ann. Missouri Bot. Gard. 79: 249–265.

PAGE, R. D. M. 1991. Random dendrograms and null hypotheses in cladistic biogeography. Syst. Zool. 40: 54–62.

———. 1993a. Genes, organisms, and areas: The problem of multiple lineages. Syst. Biol. 42: 77–84.

———. 1993b. On islands of trees and the efficacy of different methods of branch swapping in finding most-parsimonious trees. Syst. Biol. 42: 200–210.

PALMER, J. D., R. K. JANSEN, H. J. MICHAELS, M. W. CHASE & J. R. MANHART. 1988. Chloroplast DNA variation and plant phylogeny. Ann. Missouri Bot. Gard. 75: 1180–1206.

PAMILO, P. & M. NEI. 1988. Relationships between gene trees and species trees. Molec. Biol. Evol. 5: 568–583.

PATTERSON, C. 1988. Homology in classical and molecular biology. Molec. Biol. Evol. 5: 603–625.

PEDERSEN, K. R., P. R. CRANE, A. N. DRINNAN & E. M. FRIIS. 1991. Fruits from the mid-Cretaceous of North America with pollen grains of the *Clavatipollenites* type. Grana 30: 577–590.

PELLMYR, O. 1992. Evolution of insect pollination and angiosperm diversification. Trends Ecol. Evol. 7: 46–49.

PENNY, D. M., D. HENDY & M. A. STEELE. 1992. Progress with methods for constructing evolutionary trees. Trends Ecol. Evol. 7: 73–79.

PLATNICK, N. I. & V. A. FUNK (editors). 1983. Advances in Cladistics, vol. 2. Proceedings of the Second Meeting of the Willi Hennig Society. Columbia Univ. Press, New York.

———, C. E. GRISWOLD & J. A. CODDINGTON. 1991. On missing entries in cladistic analysis. Cladistics 7: 337–343.

QUEIROZ, A. DE. 1993. For consensus (sometimes). Syst. Biol. 42: 368–372.

QUEIROZ, K. DE. 1988. Systematics and the Darwinian revolution. Philos. Sci. 55: 238–259.

———. 1992. Phylogenetic definitions and taxonomic philosophy. Biol. Philos. 7: 295–313.

——— & J. GAUTHIER. 1992. Phylogenetic taxonomy. Annual Rev. Ecol. Syst. 23: 449–480.

RAUBESON, L. A. & R. K. JANSEN. 1992. Chloroplast DNA evidence on the ancient evolutionary split in vascular land plants. Science 255: 1697–1699.

REMY, W. 1982. Lower Devonian gametophytes: Relation to the phylogeny of land plants. Science 215: 1625–1627.

RIESEBERG, L. H. & S. BRUNSFELD. 1992. Molecular evidence and plant introgression. Pp. 151–176 *in* P. S. Soltis, D. E. Soltis & J. J. Doyle (editors), Molecular Systematics in Plants. Chapman & Hall, New York.

——— & J. D. MOREFIELD. Character expression, phylogenetic reconstruction, and the detection of reticulate evolution. *In* P. C. Hoch & A. G. Stephenson (editors), Experimental and Molecular Approaches to Plant Biosystematics. Monogr. Syst. Bot. Missouri Bot. Gard. (in press).

——— & D. E. SOLTIS. 1991. Phylogenetic consequences of cytoplasmic gene flow in plants. Evol. Trends Pl. 5: 65–84.

SANDERSON, M. J. 1989. Confidence limits on phylogenies: The bootstrap revisited. Cladistics 5: 113–129.

——— & M. J. DONOGHUE. 1989. Patterns of variation in levels of homoplasy. Evolution 43: 1781–1795.

——— & J. J. DOYLE. 1992. Reconstruction of organismal and gene phylogenies from data on multigene families: Concerted evolution, homoplasy, and confidence. Syst. Biol. 41: 4–17.

———, B. G. BALDWIN, G. BHARATHAN, C. S. CAMPBELL, C. VON DOHLEN, D. FERGUSON, J. M. PORTER, M. F. WOJCIECHOWSKI & M. J. DONOGHUE. 1993. The growth of phylogenetic information, and the need for a phylogenetic data base. Syst. Biol. 42: 562–568.

SAVAGE, H. M. 1983. The shape of evolution: Systematic tree topology. Biol. J. Linn. Soc. 20: 225–244.

SLATKIN, M. & W. P. MADDISON. 1990. Detecting isolation by distance using phylogenies of alleles. Genetics 126: 249–260.

SMITH, A. B. 1989. RNA sequence data in phylogenetic reconstruction: Testing the limits of resolution. Cladistics 5: 321–344.

SOBER, E. 1988. Reconstructing the Past: Parsimony, Evolution, and Inference. MIT Press, Cambridge, Massachusetts.

SOLTIS, D. E., P. S. SOLTIS & B. D. NESS. 1989. Chloroplast DNA variation and multiple origins of autopolyploidy in *Heuchera micrantha* (Saxifragaceae). Evolution 43: 650–656.

SOLTIS, P. S., D. E. SOLTIS & C. J. SMILEY. 1992. An *rbc*L sequence from a Miocene *Taxodium* (bald cypress). Proc. Natl. Acad. Sci. USA 89: 449–451.

STEBBINS, G. L. 1974. Flowering Plants: Evolution Above the Species Level. Harvard Univ. Press, Cambridge, Massachusetts.

SWOFFORD, D. L. 1991. When are phylogeny estimates from molecular and morphological data incongruent? Pp. 295–333 *in* M. M. Miyamoto & J. Cracraft (editors), Phylogenetic Analysis of DNA Sequences. Oxford Univ. Press, New York.

———. 1993. PAUP: Phylogenetic Analysis Using

Parsimony, Version 3.1. Illinois Nat. Hist. Surv., Champaign, Illinois.

——— & W. P. Maddison. 1987. Reconstructing ancestral character states under Wagner parsimony. Math. Biosci. 87: 199–229.

——— & G. J. Olsen. 1990. Phylogeny reconstruction. Pp. 411–501 *in* D. M. Hillis & C. Moritz (editors), Molecular Systematics. Sinauer Assoc., Sunderland, Massachusetts.

Sytsma, K. J. 1990. DNA and morphology: Inference of plant phylogeny. Trends Ecol. Evol. 5: 104–110.

Takahata, N. 1989. Gene genealogy in three related populations: Consistency probability between gene and population trees. Genetics 122: 957–966.

Takhtajan, A. 1987. Sistema Magnoliofitov (Systema Magnoliophytorum). Acad. Sciences, USSR, Nauka, Leningrad. [In Russian.]

———. 1991. Evolutionary Trends in Flowering Plants. Columbia Univ. Press, New York.

Taylor, D. W. & L. J. Hickey. 1992. Phylogenetic evidence for the herbaceous origin of angiosperms. Pl. Syst. Evol. 180: 137–156.

Troitsky, A. V., Y. F. Melekhovets, G. M. Rakhimova, V. K. Bobrova, K. M. Valiejo-Roman & A. S. Antonov. 1991. Angiosperm origin and early seed plant evolution deduced from rRNA sequence comparisons. J. Molec. Evol. 32: 253–361.

Tucker, S. C. 1988. Loss versus suppression of floral organs. Pp. 69–82 *in* P. Leins, S. C. Tucker & P. Endress (editors), Aspects of Floral Development. Gebrüder Borntraeger, J. Cramer, Berlin-Stuttgart.

Valdez, A. M. & D. Piñero. 1992. Phylogenetic estimation of plasmid exchange in bacteria. Evolution 46: 641–656.

Vane-Wright, R. I., C. J. Humphries & P. H. Williams. 1991. What to protect?—Systematics and the agony of choice. Biol. Conserv. 55: 235–254.

Wagner, W. H. 1980. Origin and philosophy of the groundplan-divergence method of cladistics. Syst. Bot. 5: 173–193.

Waters, D. A., M. A. Buchheim, R. A. Dewey & R. L. Chapman. 1992. Preliminary inferences of the phylogeny of bryophytes from nuclear-encoded ribosomal RNA sequences. Amer. J. Bot. 79: 459–466.

Weller, S. G., M. J. Donoghue & D. Charlesworth. The evolution of self-incompatibility in angiosperms: A phylogenetic approach. *In* P. C. Hoch & A. G. Stephenson (editors), Experimental and Molecular Approaches to Plant Biosystematics. Monogr. Syst. Bot. Missouri Bot. Gard. (in press).

Wheeler, W. C. 1990. Nucleic acid sequence phylogeny and random outgroups. Cladistics 6: 363–367.

———. 1992. Extinction, sampling, and molecular phylogenetics. Pp. 205–215 *in* M. J. Novacek & Q. D. Wheeler (editors), Extinction and Phylogeny. Columbia Univ. Press, New York.

Williams, E. G., T. L. Sage & L. B. Thien. 1993. Functional syncarpy by intercarpellary growth of pollen tubes in a primitive apocarpous angiosperm, *Illicium floridanum* (Illiciaceae). Amer. J. Bot. 80: 137–142.

Wojciechowski, M. F., M. J. Sanderson, B. G. Baldwin & M. J. Donoghue. 1993. Monophyly of aneuploid *Astragalus*: Evidence from nuclear ribosomal DNA internal transcribed spacer sequences. Amer. J. Bot. 80: 711–722.

Young, D. A. 1981. Are the angiosperms primitively vesselless? Syst. Bot. 6: 313–330.

Zimmer, E. A., R. K. Hamby, M. L. Arnold, D. A. LeBlanc & E. C. Theriot. 1989. Ribosomal RNA phylogenies and flowering plant evolution. Pp. 205–214 *in* B. Fernholm, K. Bremer & H. Jornvall (editors), The Hierarchy of Life. Elsevier, Amsterdam.

———, S. L. Martin, S. M. Beverley, Y. W. Kan & A. C. Wilson. 1980. Rapid duplication and loss of genes coding for the ∂ chains of hemoglobin. Proc. Natl. Acad. Sci. USA 77: 2158–2162.

INTEGRATION OF MORPHOLOGICAL AND RIBOSOMAL RNA DATA ON THE ORIGIN OF ANGIOSPERMS[1]

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ABSTRACT

Previous phylogenetic analyses of morphological and rRNA data indicated that Gnetales are the closest living relatives of angiosperms but gave different basal angiosperm relationships. A two-step morphological analysis of seed plants (including fossils) and angiosperms rooted the latter near Magnoliales, with tricolpate eudicots and paleoherbs (herbaceous magnoliids and monocots) forming a clade, whereas analyses of rRNA sequences rooted angiosperms among paleoherbs, with eudicots and woody magnoliids forming a clade. Experiments with a revised seed plant morphological data set raise further questions: when angiosperms are scored like different angiosperm subgroups, they associate with different outgroups, although Gnetales are their closest living relatives. To test whether morphological and rRNA data are seriously contradictory or rather complementary, with inconsistencies being a function of better resolution in different parts of the tree, we experimented with morphological and rRNA data sets including the same six extant "gymnosperm" and 12 angiosperm taxa. Both analyses again associate angiosperms and Gnetales. The morphological analysis differs from previous ones in placing Nymphaeales and monocots at the base of the angiosperms, but trees rooted next to Magnoliales are only one step less parsimonious. As in previous studies, the rRNA analysis roots angiosperms next to Nymphaeales and breaks up the eudicots. Bootstrap and decay analyses of the rRNA data show strong support for the monophyly of angiosperms and Gnetales and their sister group relationship, but low support for groupings within angiosperms. However, one or another group of paleoherbs is basal in most bootstrap trees. A combined analysis favors a paleoherb rooting, but other relationships agree with the morphological results; in particular, eudicots form a clade. The conclusion that Gnetales are the closest living relatives of angiosperms permits a wide range of morphological scenarios, depending on the arrangement of fossil outgroups. Discovery of fossils on the long branch leading to angiosperms, methods of factoring out artifacts in rooting, or molecular data on the control of floral morphogenesis in angiosperms and Gnetales may be required for further progress in unraveling the origin of angiosperms.

Recent cladistic analyses of morphological and ribosomal RNA data have led to apparently conflicting results on the position of angiosperms among seed plants, basal relationships among angiosperms, and resulting scenarios for the origin of angiosperms (Crane, 1985; Doyle & Donoghue, 1986, 1992; Donoghue & Doyle, 1989a; Zimmer et al., 1989; Loconte & Stevenson, 1990, 1991; Taylor & Hickey, 1992; Hamby & Zimmer, 1992). The purpose of this paper is to investigate the causes and significance of these conflicts, and what if any robust conclusions concerning the origin of angiosperms can be drawn from these data.

Our initial morphological analysis of seed plants (Doyle & Donoghue, 1986), which included both living and fossil taxa, treated angiosperms as a single taxon, modeled on Magnoliales and Winteraceae, following the consensus at that time. This study was designed especially to test the previous analysis of Crane (1985) and other current ideas on seed plant phylogeny, by including both characters used by Crane and conflicting similarities that he had omitted. Contrary to our expectations, but as Crane had found, this analysis indicated that seed plants are a monophyletic group, with coniferopsids (cordaites, conifers, ginkgos) derived from

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advanced "seed ferns" with platyspermic seeds and saccate pollen (roughly as proposed by Rothwell, 1982), and that angiosperms belong to an "anthophyte" clade also including Bennettitales, *Pentoxylon*, and Gnetales, which is in turn nested among so-called Mesozoic seed ferns (corystosperms, glossopterids, *Caytonia*). In response to a cladistic analysis involving only extant seed plants by Loconte & Stevenson (1990), we revised this analysis with generally similar results (Doyle & Donoghue, 1992), except for more definite placement of cycads among platysperms and more uncertainty on the position of ginkgos, which may be associated with the Permian–Triassic seed fern *Peltaspermum* instead of conifers (cf. Meyen, 1984).

A subsequent analysis of extant angiosperms (Donoghue & Doyle, 1989a), using the results of the seed plant study to polarize characters within the group, yielded trees rooted in or next to the "woody magnoliid" order Magnoliales (specifically families with granular exine structure, which excludes Winteraceae and *Austrobaileya*). This result is generally consistent with conventional views on angiosperm evolution (e.g., Takhtajan, 1969; Cronquist, 1981, 1988). The remaining angiosperms form four major clades: two other groups of woody magnoliids, (1) Laurales, including Chloranthaceae, widely discussed because of their unusually simple flowers, and (2) winteroids, including Winteraceae, Illiciales, and possibly Canellaceae; (3) dicots with tricolpate and derived pollen, later designated eudicots (Doyle & Hotton, 1991); and (4) "paleoherbs," consisting of herbaceous or semiherbaceous magnoliids (Aristolochiaceae, *Lactoris*, Piperales, Nymphaeales) and monocots. Somewhat similar results were obtained by Loconte & Stevenson (1991); the most important difference, placement of Calycanthaceae and Idiospermataceae at the base of the angiosperms, may be due to their use of Recent plants only as outgroups, since the closest outgroup, Gnetales, shares features such as opposite leaves and two-trace nodes with Calycanthales.

In contrast, analyses of partial 18S and 26S rRNA sequences from angiosperms and other extant seed plants (Hamby & Zimmer, 1992), chosen to provide a test of current morphological hypotheses, placed a series of paleoherb taxa at the base of the angiosperms (Nymphaeales, Piperales, and monocots). Woody magnoliids and eudicots formed a more derived clade, within which detailed relationships are poorly resolved. These results give a different picture of the first angiosperms: they would be herbaceous or nearly so, with palmately veined leaves and anomocytic stomata, rather than woody with pinnately veined leaves and paracytic stomata. This recalls the views of Burger (1977, 1981) on the primitive status of Piperales and/or monocots, although not in detail.

More recently, the view that the first angiosperms were "paleoherbs" was elaborated by Taylor & Hickey (1990, 1992), based on recognition of an Early Cretaceous (Aptian) paleoherb fossil from Australia and their own morphological analysis. Their tree differs in that Chloranthaceae are basal, followed by Piperaceae, which contrasts with the position of Chloranthaceae in Laurales in the analysis of Donoghue & Doyle (1989a), well removed from Piperales, and in the woody magnoliid-eudicot clade in Hamby & Zimmer (1992). This difference may be partly a result of treating correlated ovule features related to orthotropy (which was assumed to be primitive) as three separate characters, and partly a result of omitting taxa that linked groups differently in the Donoghue & Doyle analysis (e.g., Trimeniaceae, which tend to link Chloranthaceae with other Laurales: cf. Endress, 1987).

The apparent conflicts between the morphological and molecular data, especially regarding "rooting" of the angiosperms, were discussed by Donoghue & Doyle (1989b), who suggested that they may illustrate a general conclusion drawn by Hillis (1987): that conflicts between morphological and molecular results rarely reflect serious contradictions, but rather different levels of resolution of the two sorts of data in different parts of the tree. This seemed to be supported by the fact that experiments with alternative trees in the seed plant studies (Doyle & Donoghue, 1986, 1992) had shown that other positions of anthophytes within seed plants, and of angiosperms within anthophytes, were only slightly less parsimonious than the most parsimonious arrangements. For example, it was only one step less parsimonious to link angiosperms with *Caytonia* and/or glossopterids, thus breaking up the anthophytes, or to link anthophytes with coniferopsids, with Gnetales basal in anthophytes—what we called a neo-englerian arrangement. Similarly, in our morphological analysis of angiosperms (Donoghue & Doyle, 1989a), we had found trees with angiosperms rooted among paleoherbs that were only one step less parsimonious than those rooted near Magnoliales. This may therefore be a case where the morphological data are ambiguous—they favor a woody magnoliid prototype, but only slightly—whereas the molecular data point strongly in one direction, toward a paleoherb rooting, and therefore provide better evidence on relationships. In other cases, it may be the molecular data

that are ambiguous and the morphological data that are clearcut. Thus the two sorts of data may be more complementary than contradictory.

In the present study, we have attempted to address these issues by comparing results derived from morphological and molecular data for the same set of seed plant taxa, probing the strengths and weaknesses of the results with methods such as bootstrap and decay analysis, and analyzing a combined data set. The question of analyzing morphological and molecular data separately and comparing the results or combining them at the outset is a topic of ongoing debate (Kluge, 1989; Barrett et al., 1991; Donoghue & Sanderson, 1992; Bull et al., 1993; de Queiroz, 1993). One argument against combining data sets is that the greater number of molecular characters will simply overwhelm the morphological characters. However, this does not necessarily hold: if the molecular results are poorly resolved, as they often are, even a small number of morphological characters can have a decisive effect (Donoghue & Sanderson, 1992). In any case, it is possible both to analyze data sets separately and to combine them, and our results imply that this approach can give instructive results.

This study is not intended to be a comprehensive examination of "morphological" versus "molecular" data on this topic. Y. Suh (pers. comm.) has obtained different results from another part of the 26S subunit of rDNA, which roots the angiosperms between a clade including most Magnoliales and Laurales and other angiosperms. Equally different trees, with the aquatic genus *Ceratophyllum* basal and remaining angiosperms divided into tricolpate-derived eudicots and monosulcate magnoliids and monocots, have been obtained from *rbc*L sequences (Les et al., 1991; Chase et al., 1993; Qiu et al., 1993). Analyses of shorter rRNA sequences by Troitsky et al. (1991) and a smaller *rbc*L data set by Hasebe et al. (1992) have given different trees, most notably with gymnosperms as a monophyletic group. Instead of considering all these data sets, we have chosen to address the two that we know best, although we will mention briefly some preliminary analyses including *rbc*L.

Combining Previous Morphological Analyses of Seed Plants and Angiosperms

A major concern that we wish to address first is the possibility that previous inferences concerning the origin of angiosperms were compromised by circular reasoning. Perhaps the position of angiosperms in the seed plant analysis (Doyle & Donoghue, 1986) was a function of the assumption that the first angiosperms were like Magnoliales and Winteraceae. Perhaps then the basal position of Magnoliales in the angiosperm analysis (Donoghue & Doyle, 1989a) was a consequence of an incorrect identification of outgroups based on this initial assumption. For the sake of rapid progress, we split the seed plant and angiosperm problems in two. This seemed reasonable at the time: there was already strong evidence that the angiosperms were monophyletic, and there was some consensus on basic states within the group. However, we realized from the beginning that it would eventually be necessary to carry out additional analyses designed to resolve simultaneously relationships at the point where the two analyses intersect. For example, we noted that Chloranthaceae share many features with Gnetales, and that angiosperms might therefore be directly associated with Gnetales if Chloranthaceae were assumed to be primitive.

It should be recognized that conclusions derived from this sort of two-step procedure are not necessarily incorrect: there might be only one most parsimonious position for angiosperms no matter what internal relationships or basal states in angiosperms are assumed. It should also be noted that the problems are not unique to our study: ours is simply one example of a general method that Mishler (1994) calls compartmentalization. This method was also used within our angiosperm analysis (Donoghue & Doyle, 1989a), in which we did a preliminary analysis of Laurales to determine basic states in a derived subgroup referred to as "core Laurales."

These problems were recognized and addressed in a series of experiments reported by Doyle & Donoghue (1990), which combined nine angiosperm taxa with the 17 nonangiospermous groups used in Doyle & Donoghue (1992). Here we present an updated version of these experiments, which illustrate the nature of the problem and the potential value of considering both morphological and molecular evidence.

Taxa, Characters, and Analyses

The revised seed plant and angiosperm matrix, henceforth designated the nine-angiosperm analysis, is presented in the Appendix (Table 1). The angiosperm taxa were selected to represent the major clades found by Donoghue & Doyle (1989a) in trees rooted both near Magnoliales and among paleoherbs, which necessitated dividing the paleoherbs into four groups. In five cases these clades are represented by individual taxa used in Dono-

ghue & Doyle (1989a), in four by composite taxa: Magnoliales, based on *Degeneria*, Myristicaceae, Annonaceae, and Magnoliaceae ("core Magnoliales" of Donoghue & Doyle, 1989a); Piperales (Piperaceae, Saururaceae); Nymphaeales (Nymphaeaceae, Cabombaceae); and eudicots (Ranunculidae, *Nelumbo*, Trochodendrales, Hamamelidales). These are scored in terms of estimated ancestral states for the whole taxon (theoretical and practical problems in this procedure are discussed further below). Thus, where the taxon consists of two taxa included in the previous analysis and these have different stages, the group was scored as uncertain (e.g., 0/1). In the case of binary characters, where uncertain (0/1) and unknown (?) are equivalent in tree construction, we usually distinguished between the two scorings in the matrix to indicate the nature of the uncertainty, but we did not try to weed out all cases where "?" had been used for uncertainty in the previous analyses. In Magnoliales, basic states were estimated based on the previous result that *Degeneria* is the sister group of the other three taxa, which themselves form an unresolved trichotomy. Eudicots were assumed to consist of two sister clades, Ranunculidae plus *Nelumbo* and Trochodendrales plus Hamamelidales. Laurales were represented by *Austrobaileya*, which was at or near the base of the order in our previous trees, and Chloranthaceae, which are of special interest because they have been widely discussed as possible primitive angiosperms. Use of *Austrobaileya* to represent Laurales might be questioned, since it lacks many features commonly associated with the order. However, our results bear out its use in this way, since *Austrobaileya* is associated with Chloranthaceae in the trees obtained, as it was with the larger data set. Trees were rooted by including a taxon based on Devonian "progymnosperms" (*Aneurophyton*, *Archaeopteris*) as outgroup.

Characters are primarily a combination of those used in the seed plant analysis of Doyle & Donoghue (1992) and those in the angiosperm analysis of Donoghue & Doyle (1989a) that are potentially informative for the taxa under consideration. To these we added several apomorphies that potentially hold angiosperms together as a monophyletic group, either as new characters or as additional states of existing seed plant characters (e.g., three-nucleate microgametophyte, complete loss of the megaspore wall). In some cases, features that vary within angiosperms are expressed as additional states of characters recognized in seed plants as a whole (e.g., palmate leaf venation). For angiosperm characters in which there are no clearly comparable states in other seed plants, we scored the latter as unknown; this is especially true of floral characters, where we hoped to avoid biasing the results by assuming questionable homologies of parts between angiosperms and other groups. These characters also form the basis for the morphological analysis of Recent taxa presented below as a counterpart of the rRNA analysis; for simplicity we retained nine states that were potentially informative in that matrix but autapomorphic in the present one (e.g., tetracytic stomates in Piperales, tricolpate pollen in eudicots).

Multistate characters were unordered, except for two easily ordered quantitative characters (pollen size, megaspore wall thickness). Two multistate characters involving exine structure deserve special consideration, since our decision not to order them had a significant impact on the results presented below.

In the angiosperm study (Donoghue & Doyle, 1989a), we recognized an infratectal structure character with granular and columellar states and assumed that granular was primitive, based on outgroup comparison with other anthophytes. In the revised seed plant study (Doyle & Donoghue, 1992), we recognized spongy-alveolar, honeycomb-alveolar, and granular states and scored angiosperms as granular, assuming that columellar structure evolved within the group. In combining the two data sets, our previous polarization of states within angiosperms could be preserved by ordering the character (spongy–honeycomb–granular–columellar). By placing two steps between alveolar and columellar, this ordering would bias against trees in which angiosperms are linked with alveolar outgroups (e.g., *Caytonia*, glossopterids), columellar groups are basal in angiosperms, and granular structure in groups like Magnoliales is a convergence with Bennettitales, *Pentoxylon*, and Gnetales. This scenario involves four steps if the exine character is ordered but three if it is not. Such a bias might be defended based on the coexistence of columellar and granular structure (and transitional states) within angiosperms (Walker, 1976; Le Thomas, 1980–1981) and of alveolar and granular structure within conifers (Van Campo & Lugardon, 1973). However, it seems unwarranted to assume that a direct transition from alveolar to columellar could not have occurred in other cases. Trees with angiosperms linked with *Caytonia* were only one step longer than the shortest trees in terms of the Doyle & Donoghue (1986, 1992) data sets, and a transition from alveolar to granular is certainly conceivable on structural grounds (e.g., reduction of the side-walls of the alveolae, leaving

the junctions between the walls as columellae: E. Masure, pers. comm.).

Endexine structure was not included as a character in the seed plant analyses (Doyle & Donoghue, 1986, 1992), because all groups except angiosperms have a uniformly laminated endexine, making the character uninformative. Of the two states in angiosperms, endexine present or absent in the extra-apertural areas, absence of endexine was assumed to be ancestral (Donoghue & Doyle, 1989a). This was based on the hypothesis that the laminated endexine of other seed plants is homologous with the footlayer of angiosperms, since both develop from similar tangential lamellae, and that the endexine of angiosperms, which is nonlaminated except sometimes under the apertures, is a new layer (Zavada, 1984). Again, the original polarization could be preserved in the combined data set by ordering the character (endexine laminated–absent–nonlaminated). However, because the homologies involved are rather speculative (cf. Gabarayeva, 1991), it seems preferable to treat the three states as unordered.

We also made a few substantive changes based on new data, such as recognition that pollen of Piperaceae (Piperales) has supratectal spinules and a sculptured sulcus (Bornstein, 1989), Cabombaceae (Nymphaeales) have a columellar exine structure (Osborn et al., 1991), Myristicaceae (Magnoliales) have both S and PI type sieve-tube plastids, and Aristolochiaceae have basically PII type plastids (as seen in *Saruma* and *Asarum*), like monocots (Behnke, 1988). We added one new potential synapomorphy of angiosperms and Gnetales, double fertilization, in the sense of regular fusion of the second sperm nucleus with a second megagametophyte nucleus. This has been confirmed in *Ephedra* and seems independent of (although probably a prerequisite for) the uniquely angiospermous feature of endosperm formation (Friedman, 1990, 1992; Donoghue & Scheiner, 1992).

Several sets of analyses were performed using the new nine-angiosperm matrix. In one set, we analyzed the matrix with each of the nine angiosperm groups substituted individually for angiosperms. In removing the eight remaining taxa, we retained characters that then became autapomorphies; it is often desirable to remove such characters because they are uninformative and distort measures of homoplasy, but this is not a problem in the present case, where we are not concerned with relative levels of homoplasy. However, we did remove invariant characters with MacClade (Maddison & Maddison, 1992). All these data sets were analyzed with PAUP (version 3.0L, Swofford, 1991). Since there are too many taxa for branch-and-bound analysis, which guarantees finding all most parsimonious trees, we used the heuristic search algorithm, with 10 replicates of stepwise random addition of taxa and TBR branch swapping. This increases the probability of finding most parsimonious trees that belong to different "islands" (Maddison, 1991), which were in fact found in some experiments (see results). Alternative arrangements were investigated using MacClade and the constraints option in PAUP.

SINGLE-ANGIOSPERM ANALYSES

Experiments with single angiosperm taxa resulted in several different positions of the angiosperms relative to other anthophytes (*Pentoxylon*, Bennettitales, Gnetales), and of anthophytes within seed plants.

As expected, when Magnoliales are substituted for angiosperms (Fig. 1), angiosperms are the sister group of other anthophytes, and anthophytes are associated with one or another combination of *Caytonia*, glossopterids, and corystosperms, as in Doyle & Donoghue (1986, 1992). Relationships among other groups also parallel those found by Doyle & Donoghue (1992), including some with the arrangement of extant cycads, *Ginkgo*, and conifers found by Loconte & Stevenson (1990). As shown in Figure 1, one of the characters that supports this position of Magnoliales is the presence of granular exine structure.

In contrast, when Winteraceae, *Austrobaileya*, eudicots, Aristolochiaceae, or monocots are substituted for angiosperms, the angiosperm taxon connects with *Caytonia* or *Caytonia* plus glossopterids. This is also true of most trees found when Nymphaeales are substituted for angiosperms (Fig. 2), although in two such trees the Bennettitales–*Pentoxylon*–Gnetales clade, Nymphaeales, and *Caytonia* form a paraphyletic group at the base of the platysperms (a stratigraphically very unparsimonious arrangement). These trees break up the anthophytes, although the Bennettitales–*Pentoxylon*–Gnetales clade is still the next-closest group to angiosperms. This result might be questioned because it implicitly assumes that *Caytonia* and/or glossopterids had angiosperm and gnetalian states for several characters that were scored as unknown because they are not preserved or not yet established in fossils, such as lignin chemistry, a tunica layer in the apical meristem, and siphonogamy (the same is also true for Bennettitales and *Pentoxylon* in trees of the sort shown in Fig. 1). One reason for the new position of these angiosperm taxa is

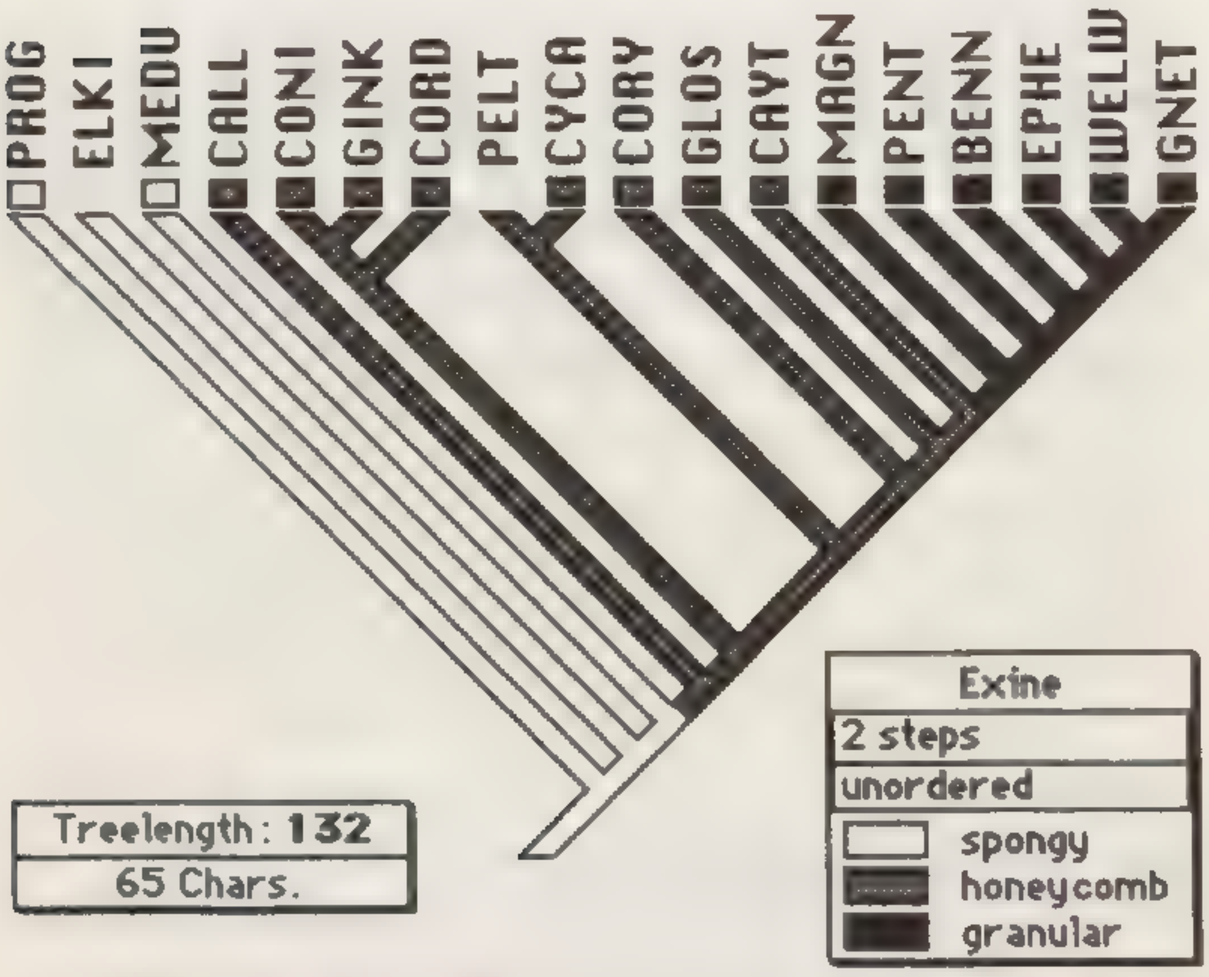

FIGURE 1. Representative most parsimonious tree (of 94) found when "core" Magnoliales (MAGN) are substituted for angiosperms as a whole in the nine-angiosperm analysis of extant and fossil seed plants. Shading of branches shows distribution of the exine structure character, which tends to link Magnoliales with other anthophytes (*Pentoxylon*, Bennettitales, Gnetales). PROG = "progymnosperms"; ELKI = *Elkinsia*; MEDU = Medullosaceae; CALL = *Callistophyton*; CONI = Coniferales; GINK = Ginkgoales; CORD = Cordaitales; PELT = *Peltaspermum*; CYCA = Cycadales; CORY = Corystospermaceae; GLOS = Glossopteridales; CAYT = *Caytonia*; PENT = *Pentoxylon*; BENN = Bennettitales; EPHE = *Ephedra*; WELW = *Welwitschia*; GNET = *Gnetum*.

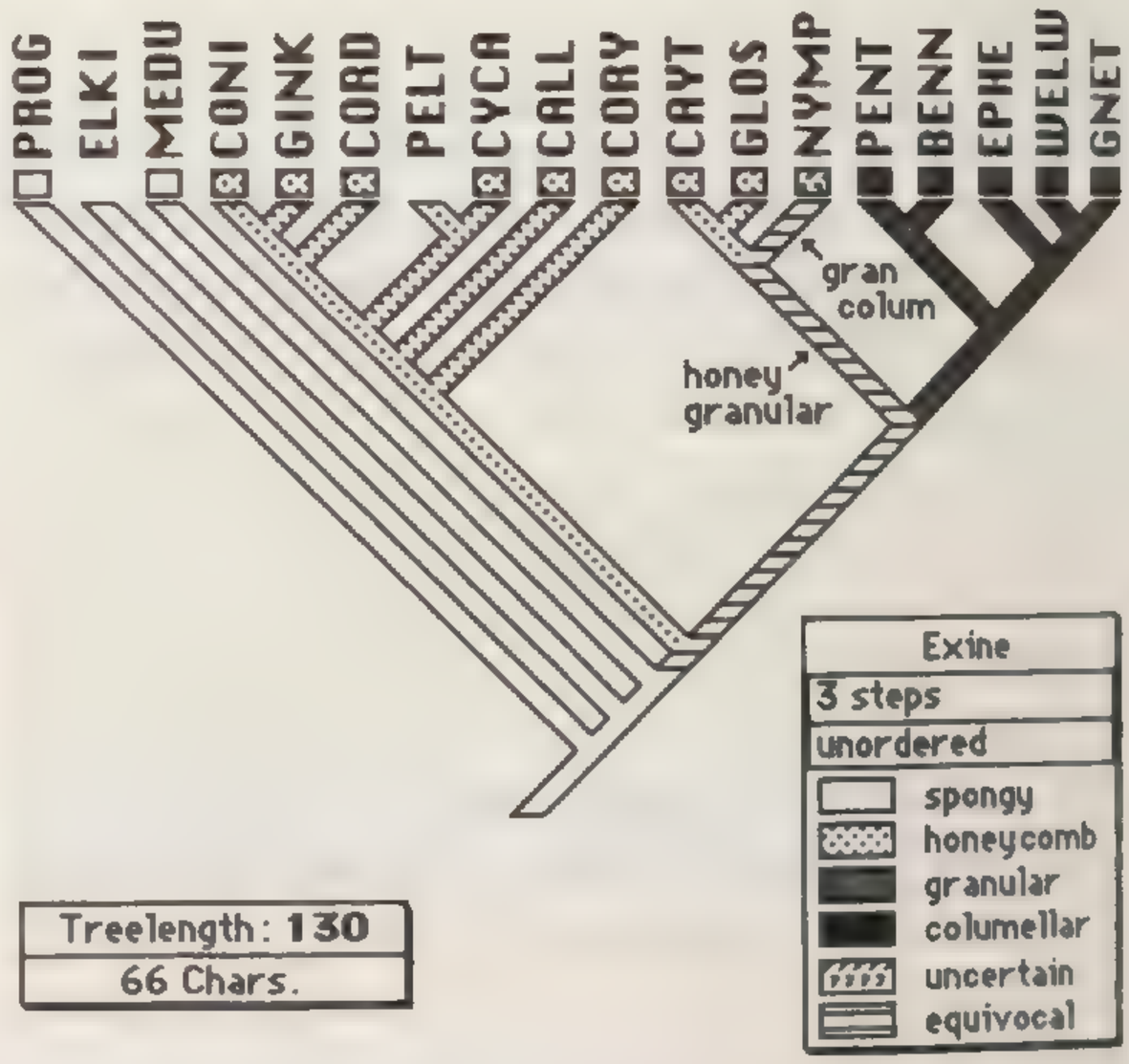

FIGURE 2. Representative most parsimonious tree (of 31) found when Nymphaeales (NYMP) are substituted for angiosperms, showing distribution of the exine structure character. Generally similar trees (some with angiosperms linked with *Caytonia* alone) are also found when Winteraceae, *Austrobaileya*, eudicots, Aristolochiaceae, and monocots are substituted for angiosperms. Arrows indicate possible exine states on branches where the state is equivocal. Other abbreviations as in Figure 1.

presumably that they have columellar rather than granular exine structure (or both columellar and granular structure in the case of Nymphaeales, which were therefore scored as uncertain), so they are not as strongly "attracted" to other granular anthophytes as Magnoliales are. The exine structure character would have tended to associate angiosperms with other anthophytes if it had been ordered, with columellar implicitly derived from granular, but it does not when it is treated as unordered. Competing characters attracting angiosperms in general to *Caytonia* are reticulate venation, flat guard cells, and anatropous cupules (scored like anatropous bitegmic ovules).

As anticipated, in most of the trees found when Chloranthaceae are substituted for angiosperms (Fig. 3a), Chloranthaceae are linked directly with Gnetales, with which they share such features as opposite leaves, two-trace nodes, spicate inflorescences (scored as compound strobili), and orthotropous ovules. In these trees, the position of anthophytes is highly unstable: they may be the sister group of other platysperms or variously associated with cycads, glossopterids, *Caytonia*, or a corystosperm–glossopterid–*Caytonia* clade. The exceptions are neo-englerian trees in which Chloranthaceae are linked with *Pentoxylon* and Bennettitales (Fig. 3b), which maintain the putative homologies between Chloranthaceae and Gnetales, such as compound strobili, as symplesiomorphies. Anthophytes are not broken up in any of these trees.

The most varied trees are found when Piperales are substituted for angiosperms. As when Chloranthaceae are the single angiosperm group, these include neo-englerian trees where Piperales are linked with *Pentoxylon* and Bennettitales and trees where anthophytes are the sister group of other platysperms. However, in trees of the latter sort Piperales are not linked with Gnetales but rather with *Pentoxylon* and Bennettitales (Fig. 4). This is presumably because Piperales have features like orthotropous and bitegmic ovules that allow them to be nested between Bennettitales and Gnetales, but not features like opposite leaves and two-trace nodes that unite Gnetales and Chloranthaceae. However, Piperales are linked with Gnetales in a few stratigraphically unparsimonious trees where anthophytes form a paraphyletic group at the base of platysperms. Finally, there are numerous trees in which Piperales are basal in anthophytes and anthophytes are nested among *Caytonia*, glossopterids, and corystosperms, analogous to trees of Doyle & Donoghue (1992) and trees found when Magnoliales are substituted for angiosperms (Fig. 1), and a few trees where Piperales are linked

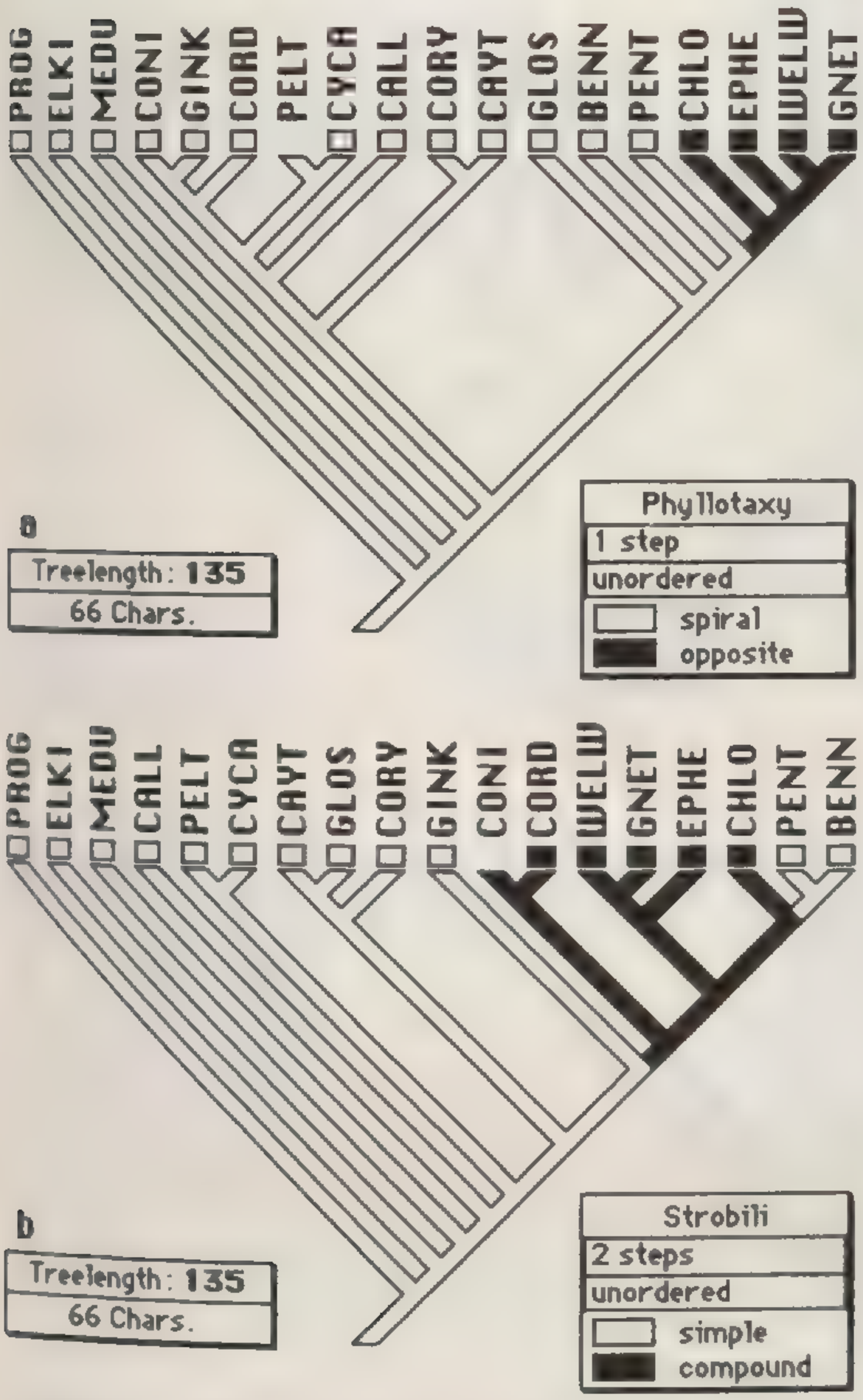

FIGURE 3. Two representative most parsimonious trees (of 166) found when Chloranthaceae (CHLO) are substituted for angiosperms, showing distribution of the phyllotaxy (a) and strobilus (b) characters; (b) is a neo-englerian tree, with anthophytes nested among "coniferopsids" (ginkgos, conifers, cordaites). Other abbreviations as in Figure 1.

directly with *Caytonia*, thus breaking up the anthophytes. Presumably, Piperales have fewer characters that support any one of these arrangements over another.

The instability of angiosperm relationships seen in these experiments is not evident when extant taxa alone are considered, since in almost all trees Gnetales are the closest living relatives of angiosperms (the exceptions are the few trees in which Nymphaeales and Gnetales form a paraphyletic group). The variations are a function of different relationships between angiosperms and various fossil taxa. However, the different trees would have very different implications for basic states and character evolution within the angiosperms, and this illustrates the severe limitations of trees based on extant taxa alone in evaluation of evolutionary scenarios, because of the gaps between extant groups. For example, trees in which angiosperms

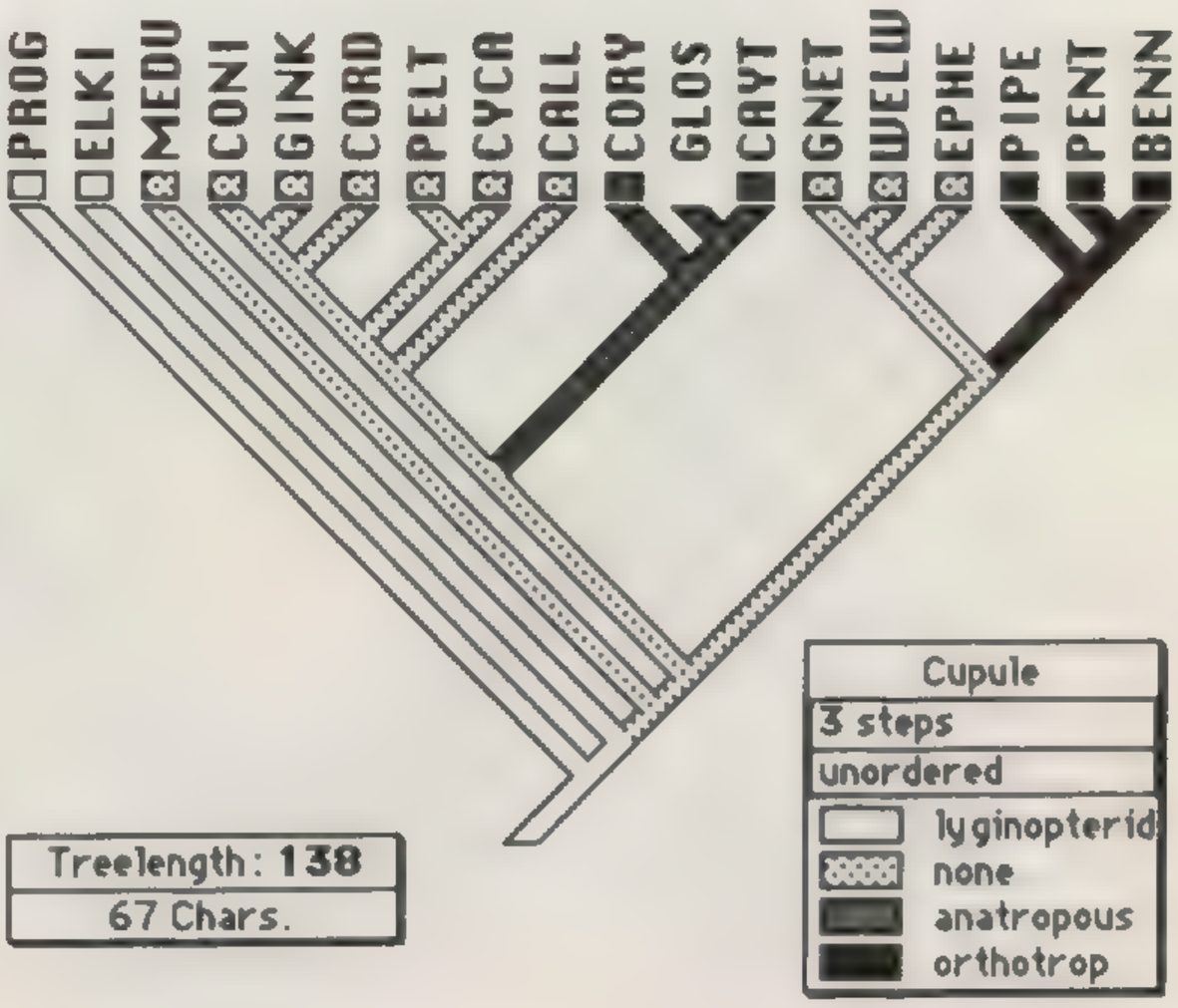

FIGURE 4. Representative most parsimonious tree (of 155) found when Piperales (PIPE) are substituted for angiosperms, showing distribution of the cupule character. Other equally parsimonious trees are more comparable to those in Figures 1, 2, and 3b. Other abbreviations as in Figure 1.

are linked with *Caytonia* and/or glossopterids imply that flowerlike reproductive structures originated independently in angiosperms and the clade consisting of Bennettitales, *Pentoxylon*, and Gnetales. Trees in which angiosperms are linked with Gnetales, and/or neo-englerian trees in which anthophytes are linked with coniferopsids and Gnetales are basal, imply that angiosperm flowers and floral parts, especially carpels containing several ovules with two integuments, were elaborated from simpler structures like those of Gnetales, or derived by aggregation of several gnetalian "flowers" (i.e., a pseudanthial interpretation).

These results bear out the concern that the position of angiosperms in previous analyses (Doyle & Donoghue, 1986, 1992) may have been incorrect because of initial assumptions about basal states in angiosperms. They also raise the possibility that angiosperms are polyphyletic, with different "angiosperm" groups related to different "gymnosperms." However, neither conclusion necessarily follows, since they depend on whether and how the various angiosperm groups link up with each other.

NINE-ANGIOSPERM ANALYSES

To assess the possibilities just raised, we included all nine angiosperm groups and analyzed the resulting matrix (35 replicates, stepwise random addition of taxa, TBR branch swapping). This analysis yielded 11 most parsimonious trees of 192 steps, which differ only in arrangements within a clade consisting of *Callistophyton*, coniferopsids, cory-

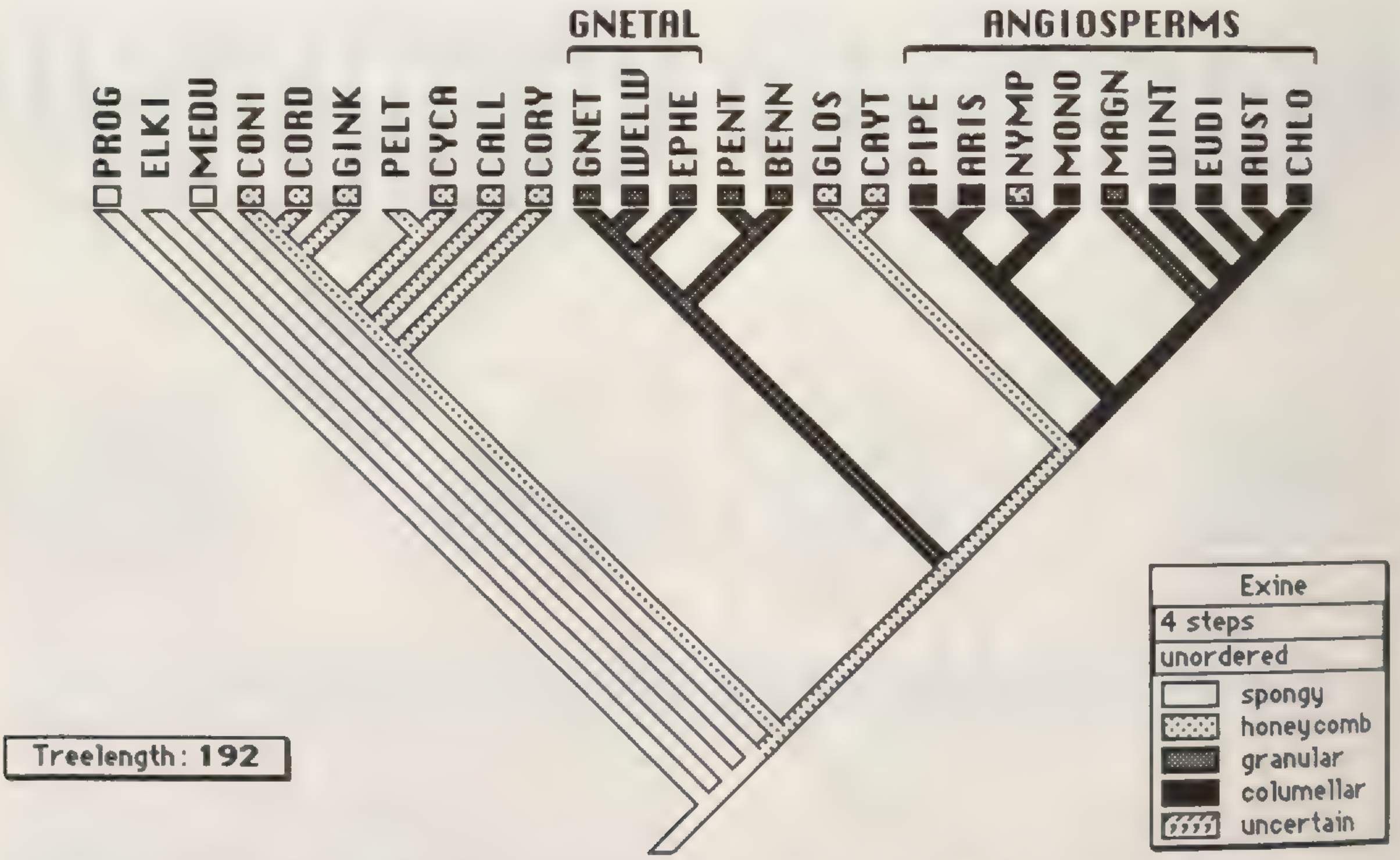

FIGURE 5. Representative most parsimonious tree (of 11) found when all nine angiosperm taxa are included in the analysis, showing distribution of the exine structure character. PIPE = Piperales; ARIS = Aristolochiaceae; NYMP = Nymphaeales; MONO = monocots; MAGN = "core" Magnoliales; WINT = Winteraceae; EUDI = eudicots (= groups with tricolpate and derived pollen); AUST = *Austrobaileya*; CHLO = Chloranthaceae; other abbreviations as in Figure 1.

stosperms, *Peltaspermum*, and cycads (e.g., Fig. 5). In these trees, angiosperms form a monophyletic group, and Gnetales are their closest living relatives. However, in contrast to trees of Doyle & Donoghue (1986), where angiosperms are the sister group of other anthophytes, angiosperms are linked with *Caytonia* and glossopterids, as when Winteraceae, *Austrobaileya*, eudicots, and some paleoherbs were substituted for angiosperms (Fig. 2). Furthermore, the arrangement within angiosperms differs from any seen previously: they split into one clade consisting of paleoherbs (including monocots) and another consisting of woody magnoliids and eudicots. As with trees where single angiosperm taxa were associated with *Caytonia* and/or glossopterids, this rearrangement is presumably influenced by treatment of the exine structure and endexine characters as unordered. This change in character analysis weakens the tendency of angiosperms to associate with the granular Bennettitales–*Pentoxylon*–Gnetales clade, with granular Magnoliales attached between the latter and columellar angiosperms.

Although these results cast doubt on previous inferences regarding the origin of angiosperms, the change from the previous situation is less radical than it seems. Essentially the same alternative relationships recognized as almost equally parsimonious by Doyle & Donoghue (1986, 1992) and Donoghue & Doyle (1989a) are seen among one step less parsimonious ("one-off") trees (193 steps) (Fig. 6). Some of these trees show the sorts of relationships that were most parsimonious in the previous analyses, in which anthophytes are associated with *Caytonia* and glossopterids, angiosperms are the sister group of other anthophytes, and Magnoliales are basal in angiosperms (Fig. 6a). As in the previous analyses, other one-off trees are of the neo-englerian type (Fig. 6b), in which anthophytes are linked with coniferopsids, and Gnetales, with linear leaves and simple sporophylls, are basal and relatively plesiomorphic in anthophytes. In other 193-step trees, Nymphaeales are basal in angiosperms, as inferred from rRNA data (Hamby & Zimmer, 1992); in fact, some of these have the same arrangement of paleoherb taxa found in the rRNA analyses presented below, with Piperales next above Nymphaeales and monocots linked with Aristolochiaceae (Fig. 6c). Given the minimal differences in parsimony, it would be unwarranted to conclude that the tree in Figure 5 should now be strongly preferred over those in Donoghue & Doyle (1989a) or Doyle & Donoghue (1992). Although the shift away from a basal position of Magnoliales may represent real progress, reflecting as it does the removal of previous biases in exine characters,

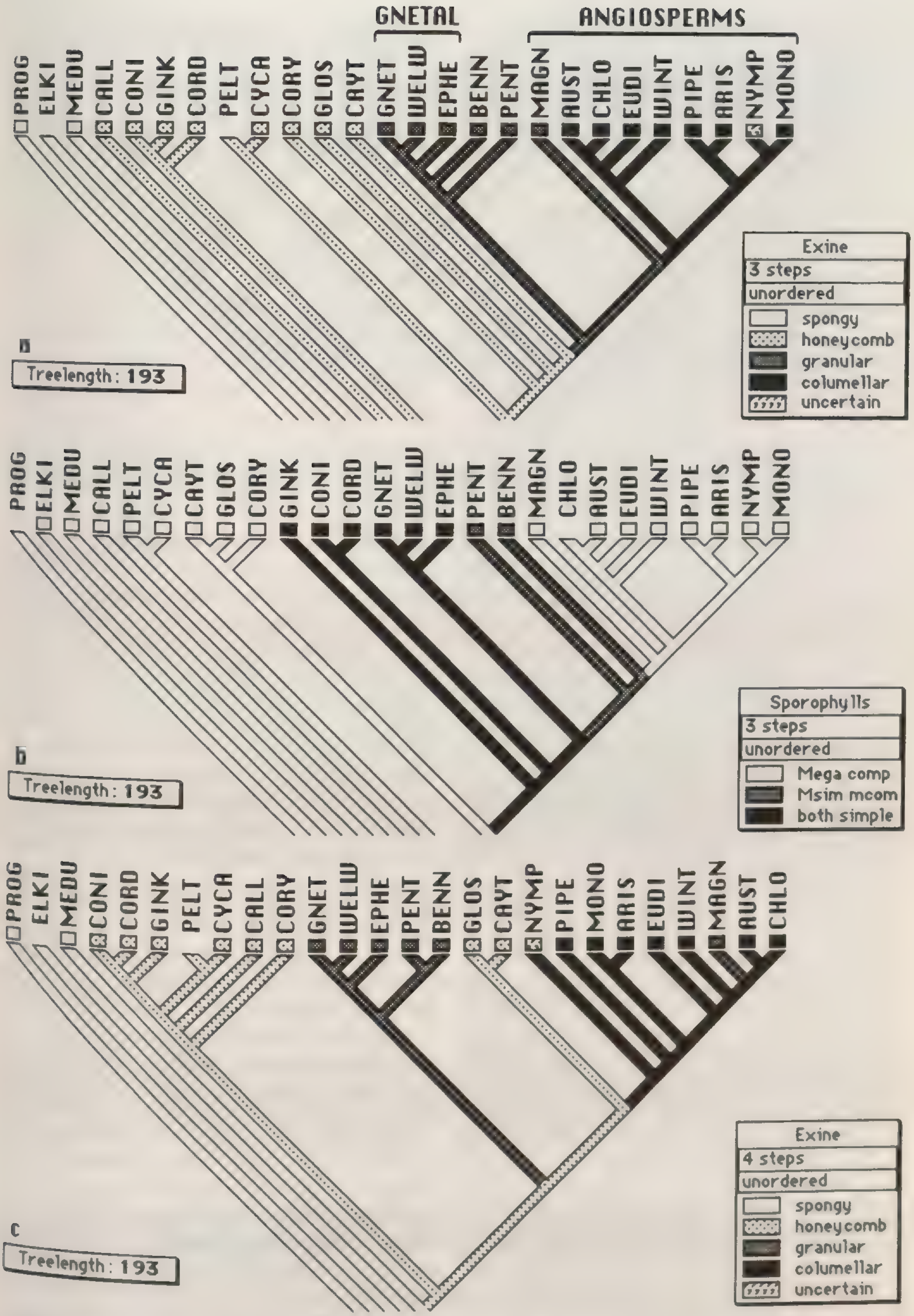

FIGURE 6. Representative one step less parsimonious (one-off) trees found with the nine-angiosperm data set: (a) with angiosperms the sister group of other anthophytes and Magnoliales basal in angiosperms, as in Doyle & Donoghue (1986, 1992) and Donoghue & Doyle (1989a), showing distribution of the exine structure character; (b) neo-englerian tree, with anthophytes nested among "coniferopsids," showing distribution of the sporophyll character; (c) with angiosperms linked with *Caytonia* and glossopterids and Nymphaeales basal in angiosperms, as in trees based on rRNA data, showing distribution of the exine structure character. Abbreviations as in Figures 1 and 5.

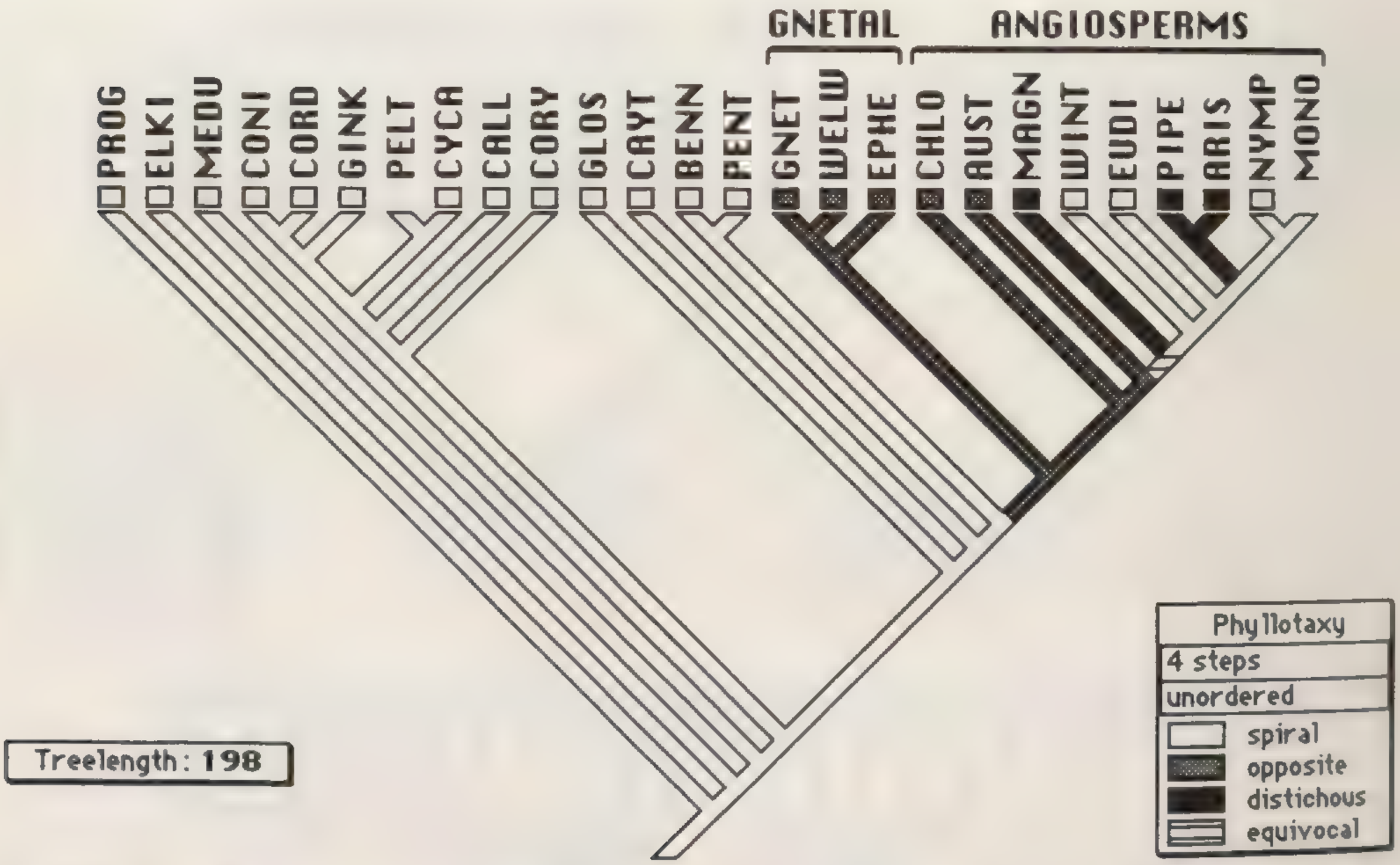

FIGURE 7. Representative tree (of 1675) found when angiosperms and Gnetales are forced together and Chloranthaceae are forced to the base of angiosperms, showing distribution of the phyllotaxy character. This tree is six steps less parsimonious than the shortest trees. Abbreviations as in Figures 1 and 5.

it may be as much a function of the smaller number of taxa and the omission of connecting groups.

Despite these ambiguities, experiments with alternative topologies do provide some stronger results. The most interesting experiments concern proposed links between Gnetales and Chloranthaceae. Trees with angiosperms forced together with Gnetales using the constraints option in PAUP are only two steps longer than the shortest trees, but Chloranthaceae are not basal in angiosperms, as might be expected from their gnetalian features; instead, angiosperms are arranged as in the most parsimonious trees (Fig. 5). The shortest trees with Chloranthaceae basal in angiosperms and angiosperms linked with Gnetales (Fig. 7) are six steps longer than the shortest trees. Similarly, in the neoenglerian trees (Fig. 6b), anthophytes are not arranged in such a way that the similarities between Gnetales and Chloranthaceae are homologous; instead, angiosperms are linked with Bennettitales, and Magnoliales are basal in angiosperms.

The reason that trees of the type in Figure 7 are so unparsimonious, even though Chloranthaceae are associated with Gnetales when they are the only angiosperms in the analysis, is presumably that Chloranthaceae are "screened off" from having an influence on the position of angiosperms by being linked with *Austrobaileya* and other groups, based on such features as laterocytic stomates and globose pollen with reticulate sculpture and a verrucate sulcus. Similarly, Piperales are nested among other paleoherbs based on herbaceous habit, distichous leaves, palmate venation, and globose pollen. Of the potential homologies of Chloranthaceae and Gnetales, opposite leaves and two-trace nodes are unequivocally primitive in angiosperms in trees like Figure 7, since they also occur in *Austrobaileya*. However, compound strobili would have to be lost below *Austrobaileya*, so it is equally parsimonious to assume that this feature originated independently in Chloranthaceae and Gnetales. Other "gnetalian" features of Chloranthaceae are problematical morphologically and were therefore scored as unknown (e.g., whorled microsporophylls, one ovule per carpel). As a result, they are consistent with a link between Chloranthaceae and Gnetales when Chloranthaceae alone are substituted for angiosperms, but they do not "attract" Chloranthaceae to the base of angiosperms when all nine angiosperm taxa are included. Finally, although Chloranthaceae are like Gnetales in some respects, Magnoliales are more like Gnetales in others (e.g., leaves without chloranthoid teeth; boat-shaped pollen; tectate, granular exine structure).

The strongest conclusion of these analyses is that both angiosperms and Gnetales are monophyletic groups. In the tree shown in Figure 5, they are unambiguously supported by nine and eight

characters, respectively. Four of the angiosperm synapomorphies are universal in the group (or represented by clearly related states) and unknown elsewhere (two pairs of pollen sacs, endothecium, stigmatic pollen germination, loss of megaspore wall). Of the five others, vessels and several vein orders arose independently in Gnetales, scalariform secondary xylem in Bennettitales and *Pentoxylon*; columellae and nonlaminated endexine are not universal in angiosperms but are basic with this arrangement. Four other features that are known only in angiosperms are equivocal as angiosperm synapomorphies because the corresponding characters are unknown in *Caytonia* and glossopterids (companion cells, three-nucleate microgametophyte, eight-nucleate megagametophyte, endosperm formation). To evaluate the strength of this result, we removed angiosperm apomorphies to see at what point the group would break up. Remarkably, even when we removed all eight features that are known only in angiosperms, angiosperms still stayed together as a clade. Apparently there are enough overlapping similarities within angiosperms, such as trilacunar nodes, columellar exine structure, oil cells in most magnoliids, and palmate venation in paleoherbs and eudicots, to hold them together.

To some, this result may seem trivial, but even recently some authors have expressed the opinion that angiosperm monophyly is a pernicious dogma that has held back progress in understanding the origin of angiosperms (e.g., Hughes & McDougall, 1990; Krassilov, 1991). Similarly, the view that Gnetales are polyphyletic is still frequently encountered (e.g., Gifford & Foster, 1989). Our results imply that the assumption that angiosperms are monophyletic is not an obstacle to progress in this field, but incorrect assumptions concerning the morphology of the first angiosperms (an inappropriate "search image") might well be.

These results underline a general problem in studying modern groups that are separated from their closest relatives by "long branches": the more characters that unite the group, the more certain is its monophyletic status, but the less certain is its position. This is because spurious convergences, reversals, or changes leading to uninterpretability of characters on the long branch may obscure true relationships (Felsenstein, 1978). This effect has been most often stressed in connection with molecular characters, where there are only three alternative states to which a base at any position can change, but it may also apply to morphological characters (cf. Wake, 1991). For the same reasons, rooting of the group may be ambiguous, because the closest outgroups are so distant that they provide little "signal" as to which subgroups are basal (Wheeler, 1990). This problem is reflected in the large number of angiosperm characters that could not be polarized by outgroup comparison in Donoghue & Doyle (1989a), or could not be scored outside of angiosperms in the present analysis, and it is magnified by the large number of missing characters in fossils. As discussed in greater detail elsewhere (Doyle & Donoghue, 1993), the problem might be solved by discovery of fossils on the long branch leading to angiosperms (i.e., non-angiospermous angiophytes, or stem angiophytes, in the terminology of Doyle & Donoghue, 1993). However, although there are a few candidates, like the Late Triassic Crinopolles pollen group described by Cornet (1989a), which has angiospermlike reticulate sculpture and columellae but a gymnospermlike endexine (cf. Doyle & Hotton, 1991), there are still no fossils with angiosperm states in some characters and more plesiomorphic states in others that can be placed with certainty on the angiosperm stem lineage.

Morphological and rRNA Analyses of Extant Groups

The relationship of these results to those obtained from rRNA sequences is addressed more directly by our analyses of morphological and rRNA data from the same taxa. Since position and rooting of the angiosperms are ambiguous with the morphological data set just presented, and since still other results have been obtained with other interpretations of angiosperm characters (Loconte & Stevenson, 1991; Taylor & Hickey, 1992), one of the motivations for this study was to determine what if any additional insights into these questions can be extracted from rRNA data. Although molecular data have the disadvantage of being available only from living groups (except for a few recent fossils: e.g., Golenberg et al., 1990), whereas morphological data may exist for key fossil taxa that attach to the long branches separating extant groups (Donoghue & Doyle, 1989b; Donoghue et al., 1989), molecular data have the advantage of being independent of the seemingly endless controversies over interpretation of the morphological homologies of angiosperm structures.

Taxa, Characters, and Analyses

The starting point for our rRNA analyses was a successor to the 60-taxon data set of Hamby & Zimmer (1992), enlarged to include 71 taxa. Complete sequences are available from GenBank (Ac-

cession Nos. M81965-M82800) and the NMNH Gopher Server under "LMS." Our morphological data set is derived from the nine-angiosperm analysis described above, modified by inclusion of somewhat different angiosperm taxa and removal of fossil groups (Appendix).

We encountered a variety of problems in obtaining comparable taxa for the morphological and rRNA analyses and combining the two data sets. This required many compromises and approximations. All of these involve a certain risk of error, but we feel they are unavoidable if progress is to be made at this point (cf. Maddison & Maddison, 1992). The important thing is to spell out the assumptions involved so that they can be scrutinized and tested in future analyses.

In reducing the morphological and molecular data sets to a comparable set of taxa, our goal was to include an adequate sampling of critical taxa (as judged from results of previous studies) while keeping the number of taxa small enough for the more time-consuming analyses. We had to omit taxa for which rRNA data are still lacking; this is often unfortunate, since current evidence suggests that some such groups constitute important links. Examples are *Lactoris*, which recent authors have linked with Piperales (Carlquist, 1990) or Aristolochiaceae (Donoghue & Doyle, 1989a; Qiu et al., 1993), and *Austrobaileya*, Trimeniaceae, and *Amborella*, which may help to tie together Laurales and strengthen the position of Chloranthaceae in this group. We did not include *Ceratophyllum* (also omitted by Donoghue & Doyle, 1989a), because its position was highly unstable in the complete rRNA analyses (Hamby & Zimmer, 1992) and so many of its morphological characters are difficult to interpret. Although *Ceratophyllum* occupies a key position at the base of the angiosperms in *rbc*L analyses of seed plants as a whole (Les et al., 1991; Chase et al., 1993), its position is unstable in unrooted *rbc*L analyses of angiosperms alone (Qiu et al., 1993), suggesting that its basal position may be an artifact of long branch attraction (cf. Donoghue, 1994).

Similarly, we did not include any non-seed plants as outgroups, since outgroups in the original data sets were different. In the morphological analyses of extant seed plants (Doyle & Donoghue, 1987, 1992), we assumed that ferns and *Equisetum* are closer to extant seed plants and lycopsids more distant, but the outgroups included in the rRNA analysis were *Equisetum* and *Psilotum*. In addition, all extant outgroups are very distant from seed plants; the really appropriate outgroups are Devonian "progymnosperms" and Carboniferous "seed ferns." There is therefore reason to fear that any rooting obtained from extant outgroups might be an artifact of spurious long branch attraction (Wheeler, 1990; Maddison et al., 1992). The resulting trees are therefore unrooted networks, with the root arbitrarily placed along the branch leading to cycads. However, it will be seen that this procedure does provide instructive contrasts, because trees derived from the morphological and rRNA data sets are topologically different.

In combining original taxa into larger groups, we generally accepted clades that appeared in both the morphological analysis of Donoghue & Doyle (1989a) and the consensus of most parsimonious and one-off rRNA trees, with a few exceptions motivated by a desire to test current hypotheses. Thus we retained Piperaceae and Saururaceae as separate taxa, even though they were strongly linked in the trees of Donoghue & Doyle (1989a) and associated in some one-off rRNA trees, because they are separated in the tree of Taylor & Hickey (1992). Conversely, we combined *Hedycarya* (Monimiaceae) and *Persea* (Lauraceae) as "core Laurales" in the rRNA analysis, even though they are not associated in all most parsimonious rRNA trees, because their relationship is strongly supported and uncontroversial on morphological grounds.

Despite our efforts, taxa in the morphological and rRNA data sets are not perfectly comparable, except perhaps when they are monotypic (i.e., *Ginkgo*, *Welwitschia*). In general, clades in the morphological data set are represented in the molecular data set by a few species that show only part of the variation in the whole clade (e.g., Magnoliales by *Asimina*, *Magnolia*, and *Liriodendron*; core Laurales by *Persea* and *Hedycarya*), or by single "exemplar" species (Chloranthaceae by *Chloranthus*; Ranunculidae by *Ranunculus*; Trochodendrales by *Trochodendron*). One solution would be to rescore taxa in the morphological data set to correspond exactly to the species in the rRNA analysis. However, we opted instead to score clades as in the earlier morphological analysis and to assume that they are adequately represented in the rRNA analysis by the exemplars, since it seemed unlikely that rescoring them would lead to significantly different results in the new morphological analysis. For example, *Ranunculus* and *Trochodendron* have most of the characters that helped link Ranunculidae, Trochodendrales, and other eudicots in the previous analysis (tricolpate pollen, sculptured aperture membranes, chloranthoid teeth, lack of oil cells), plus one that would be ambiguous if Ranunculidae as a whole were considered, be-

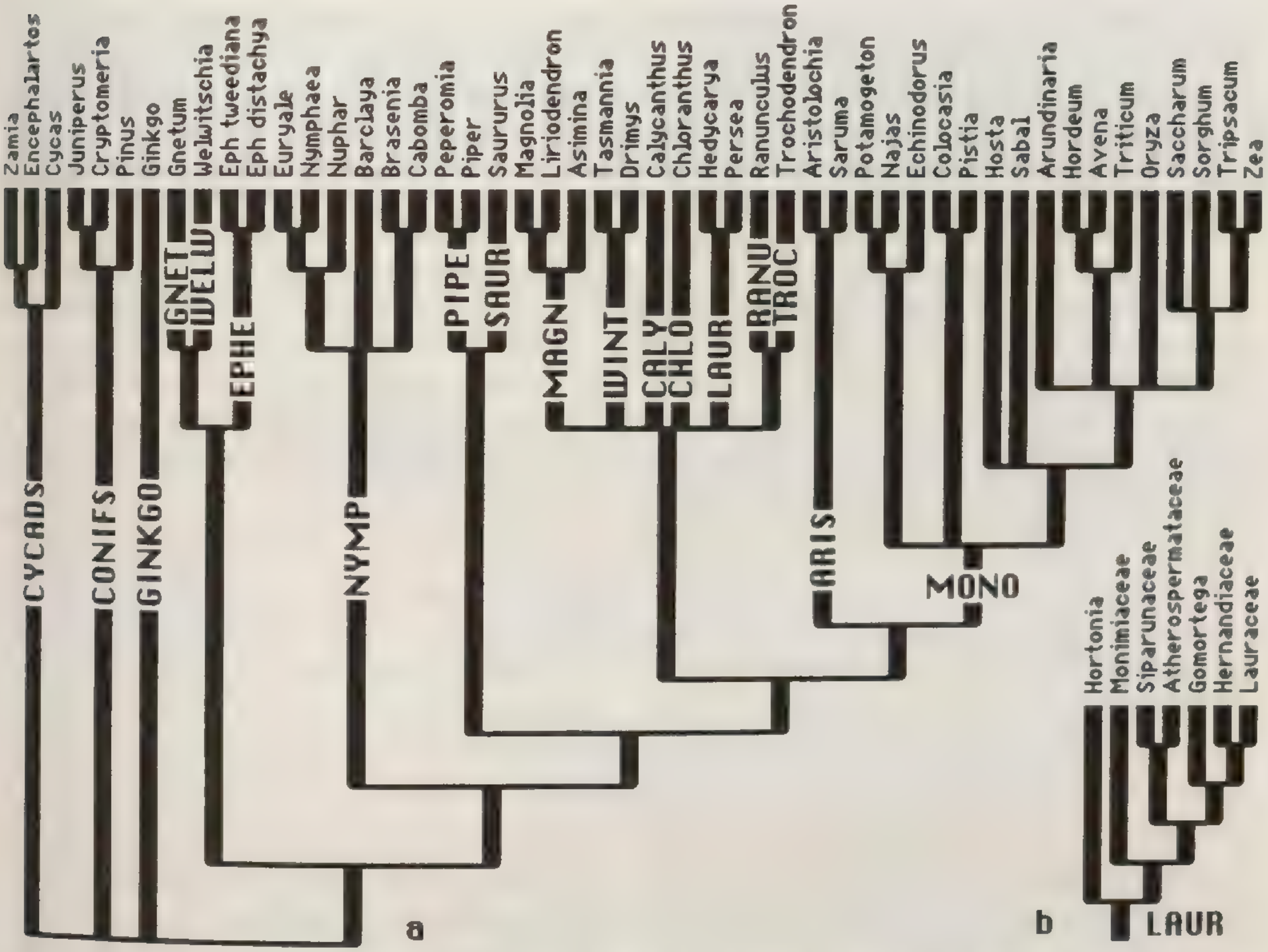

FIGURE 8. (a) Relationships assumed in reducing taxa in the original 71-taxon rRNA data set to the 18 taxa used in the present rRNA anlayses (see text for discussion). CYCADS = Cycadales; CONIFS = Coniferales; GINKGO = *Ginkgo*; GNET = *Gnetum*; WELW = *Welwitschia*; EPHE = *Ephedra*; NYMP = Nymphaeales; PIPE = Piperaceae; SAUR = Saururaceae; MAGN = "core" Magnoliales; WINT = Winteraceae; CALY = Calycanthaceae; CHLO = Chloranthaceae; LAUR = "core" Laurales; RANU = Ranunculidae; TROC = Trochodendrales; ARIS = Aristolochiaceae; MONO = monocots. (b) Relationships within core Laurales assumed in the morphological analyses.

cause of variation within that group (stamens with well-differentiated filaments).

In scoring taxa that vary for characters included in the matrix, our goal was to obtain the best estimate of ancestral states for the whole taxon. In the rRNA data set, we accepted internal relationships that were consistent in the original 71-taxon rRNA analysis and in morphological analyses by ourselves and others (Fig. 8a). For example, considering taxa included in the analysis, we assumed that *Cycas* is the sister group of *Zamia* and *Encephalartos*, and *Pinus* is the sister group of *Juniperus* and *Cryptomeria*, since these relations are found in the whole rRNA analysis and in the morphological analyses of Hart (1987), Crane (1988), and Stevenson (1990). In contrast, in Nymphaeales the rRNA data indicate that *Barclaya* is the sister group of the remaining taxa, but morphological data (Ito, 1987) imply that Cabombaceae occupy this position; therefore we treated the three groups as a trichotomy. In estimating basic states for monocots, we accepted relationships among grasses that are consistent with rRNA and morphological analyses (Kellogg & Campbell, 1987), treated *Hosta*, *Sabal*, and grasses as a trichotomy, and treated alismids, aroids, and the *Hosta*–*Sabal*–grass clade as a trichotomy. In the morphological data set, we inferred states for core Magnoliales based on the assumption that *Degeneria* is the sister group of Myristicaceae, Annonaceae, and Magnoliaceae (cf. above); in core Laurales, we assumed relationships shown in Figure 8b, derived from an unpublished analysis of Laurales used for the same purpose by Donoghue & Doyle (1989a).

The use of parsimony in optimization of ancestral states on trees is discussed by Swofford & Maddison (1987). As in the nine-angiosperm analysis, when clades consisted of two taxa that varied at a given site, we coded them as uncertain. When there were three taxa, and the "outer" taxon and one of the two "inner" taxa had the same state,

we interpreted this state as ancestral; but when the outer taxon differed from both inner taxa, we scored the clade as uncertain. In more complicated cases, we used MacClade (Maddison & Maddison, 1992) to find the most parsimonious ancestral state, taking into account all possible resolutions of trichotomies and polychotomies.

The practice of including variable taxa and scoring ancestral states as uncertain has been criticized by Nixon & Davis (1991). In the absence of homoplasy, the main effect of scoring taxa as uncertain is lowered resolution, but Nixon & Davis presented theoretical cases where uncertainties combined with homoplasy lead to incorrect trees, a danger discussed in greater depth by Maddison & Maddison (1992: 47–49). The alternative proposed by Nixon & Davis (1991) is to split up variable taxa into units that are monomorphic in terms of the characters used (a procedure with risks of its own: Maddison & Maddison, 1992; Donoghue, 1994). However, in practice Nixon et al. (1994) used smaller taxa as exemplars for larger clades. As illustrated graphically by the experiments described above, where we obtained widely varying trees when we substituted different subgroups for angiosperms as a whole, this approach is ridden with as many implicit assumptions and potentials for error (e.g., that convergences and reversals in the exemplar will not affect its position) as attempts to reconstruct basal states (Donoghue, 1994). Splitting up variable taxa into all potentially relevant monophyletic taxa might be the ideal solution, but if carried to its logical conclusion this would quickly lead to computational paralysis. In the meantime, we prefer to make explicit assumptions about basal states of the sort described, while emphasizing that these assumptions can and should be tested in the future.

Our morphological data set is presented in Table 2 (Appendix). Characters are the same as those in the nine-angiosperm analysis; changes in the number and/or definition of states as a result of removal of fossils are indicated in the character definitions. Deletion of characters that became uninformative after removal of fossil taxa left a total of 69 characters. This data set therefore parallels the extant seed plant matrix of Doyle & Donoghue (1992).

The rRNA data set is presented in Table 3 (Appendix). Characters from the 18S subunit are keyed to the corresponding positions in soy, characters from the 26S subunit to positions in rice. As a result of reducing the number of taxa from 71 to 18 and eliminating characters that became uninformative, the number of characters was reduced from 411 to 174, of which 167 are base substitutions and seven are insertion-deletion events (indels). We included the indels in the analysis because they are all of short length (five involve single nucleotides, one a dinucleotide, one a tetranucleotide: see Appendix) and because the flanking sequences leave no ambiguity as to their alignment.

All three data sets were analyzed with the heuristic algorithm in PAUP (Swofford, 1991), with 100 replicates of stepwise random addition of taxa and TBR branch swapping. Alternative topologies were investigated with the constraints option in PAUP and with MacClade (Maddison & Maddison, 1992).

One method used to evaluate the relative strength of various results is bootstrap analysis (Felsenstein, 1985). Characters are sampled randomly from the original data set with replacement and trees are calculated for the new data set, and this procedure is replicated many times. The original concept was that the frequency of bootstrap replicates in which a clade occurs is an estimate of its statistical significance: e.g., if two taxa are united in 95 out of 100 replicates, their relationship can be accepted at a 95% confidence level. Whether bootstrap frequencies should be interpreted in this way is a matter of debate (Carpenter, 1992; Hillis & Bull, 1993; Felsenstein & Kishino, 1993), but the criticisms made do not call into question the value of bootstrap analysis as a means of evaluating the relative robustness of clades. Actually, simulation experiments suggest that the bootstrap errs on the side of being conservative; under many circumstances, clades seen at bootstrap levels lower than the conventional limit of 95% are more accurate than the bootstrap numbers would imply (Hillis & Bull, 1993). In addition, bootstrap analysis may be useful in uncovering possible alternative relationships, as seen in the dot-plots of "frequency of occurrence" of groups provided by PAUP. If a link seen in the most parsimonious trees is actually due to convergence, there should also be minority characters that reflect the true relationship, and these should be sampled and amplified in a relatively high frequency of bootstrap replicates. For each data set, we did 1000 bootstrap replicates. To increase the probability of finding most parsimonious trees in each replicate, we did 10 heuristic analyses with stepwise random addition of taxa and TBR branch swapping.

The other method we employed to evaluate robustness is decay analysis (Bremer, 1988; Donoghue et al., 1992). This method determines how much longer trees have to be—how much parsimony has to be relaxed—before trees are found

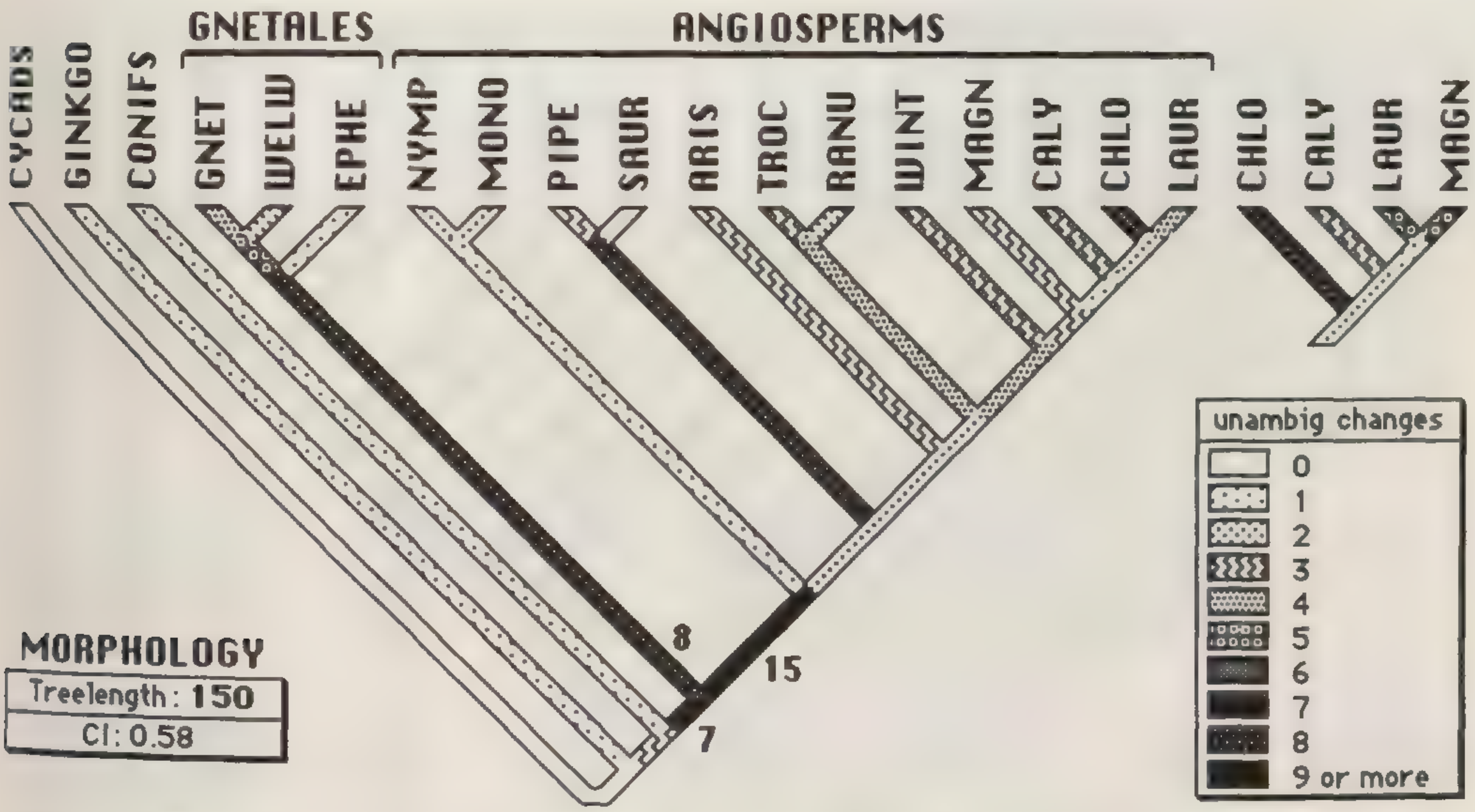

FIGURE 9. Two of the four most parsimonious trees found in analysis of the extant morphological data set, showing the number of unambiguous changes supporting each clade. Abbreviations as in Figure 8.

in which a given clade breaks up. With PAUP, this is accomplished by retaining all trees equal to or less than a given length, constructing a strict consensus of the resulting trees, and observing which clades remain in the consensus. Ideally, this is done with a branch-and-bound algorithm, which guarantees finding all trees of a given length; because this was not possible with 18 taxa, we used a heuristic search with 100 replicates of stepwise random addition and TBR branch swapping.

RESULTS OF MORPHOLOGICAL ANALYSES

Analysis of the morphological data set yields four most parsimonious trees of 150 steps, two illustrated in Figure 9. The variations concern whether Magnoliales are the sister group of the three lauralian taxa or nested among them. Figure 9 also shows the number of characters that unequivocally support clades; angiosperms are united by at least fifteen characters, Gnetales by eight, and the two groups by seven. This gives some indication of the level of support, but it is potentially misleading because it says nothing about the distribution of homoplasy—whether these changes are unique or duplicated elsewhere on the tree. This problem is addressed by the bootstrap and decay analyses. The consistency index is 0.58, about average for this number of taxa (Sanderson & Donoghue, 1989); the retention index is 0.73.

These trees show the arrangement of non-angiospermous groups found in analyses of extant taxa alone by Loconte & Stevenson (1990) and Doyle & Donoghue (1992). Doyle & Donoghue (1992) argued that this result may be an artifact of omitting fossils: when fossils are included in the analysis, this arrangement of living groups is only one of several that are equally parsimonious. In addition, several of the characters that apparently unite angiosperms are not unique to the group when fossil taxa are considered, since they also occur in *Caytonia* (flat stomata, anatropous cupules), Bennettitales (scalariform metaxylem), or both (pinnate sporophyll organization, integument free from nucellus). The whorled microsporophylls and tubular micropyle that apparently unite Gnetales are shared with Bennettitales. Of the characters uniting angiosperms and Gnetales, opposite phyllotaxy and vessels are not synapomorphies if Bennettitales and *Pentoxylon* are interpolated between the two groups.

Contrary to Donoghue & Doyle (1989a), the four most parsimonious trees root angiosperms among paleoherbs rather than Magnoliales, with Nymphaeales plus monocots as the sister group of other angiosperms. Plesiomorphic features of Nymphaeales and monocots include boat-shaped pollen and lack of oil cells (although the latter may not be valid if *Acorus*, which has oil cells, is basal in monocots, as inferred from *rbc*L data: Duvall et al., 1993). However, the conflict with the Donoghue & Doyle results is less severe than it appears: if angiosperms are rerooted on the branch to Magnoliales, only one step longer trees are obtained

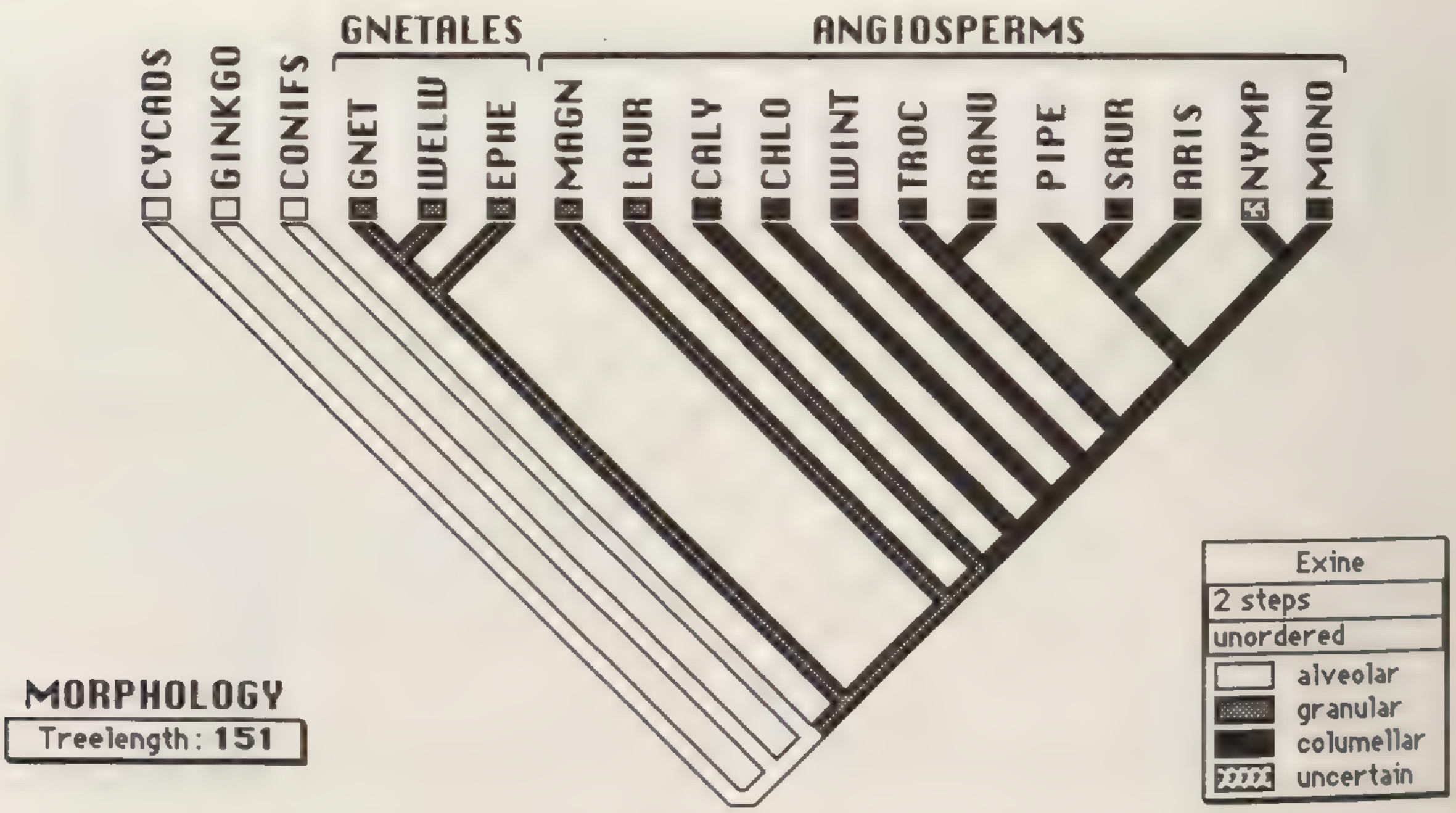

FIGURE 10. A one step less parsimonious tree based on the morphological data set with Magnoliales basal in angiosperms, showing distribution of the exine structure character. Abbreviations as in Figure 8.

that are almost entirely consistent with trees in Donoghue & Doyle (1989a), except that Laurales are paraphyletic rather than monophyletic (Fig. 10), and only one additional step is required to make Laurales a clade. The association of Magnoliales with core Laurales, either as a clade or a basal paraphyletic group, is due to possession of PI type sieve-tube plastids, granular exine structure, and a continuous tectum, all features that appear to be convergent when more taxa are included (Donoghue & Doyle, 1989a). Although monocots are associated with Nymphaeales rather than Aristolochiaceae, as in the rRNA analyses presented below, trees in which monocots are linked with Aristolochiaceae are only one step less parsimonious.

This shift in rooting may be partly a function of the smaller sampling of taxa, but as we argued above in connection with the nine-angiosperm analysis, it is also a result of treating the exine structure and endexine characters as unordered rather than implicitly ordered. Although the new morphological results are more consistent with the rRNA results, the situation does not contradict the view that the previous conflict between trees derived from the two sorts of data was a function of lower resolution of the morphological evidence—actually, it strengthens this view. Previously, morphological data favored a magnolialian rooting, but only weakly; now both data sets favor a paleoherb rooting, but the morphological data do so weakly. The fact that this shift followed from a rather subtle change in interpretation of two characters underlines the ambiguity of the morphological data.

Figure 11 summarizes the bootstrap and decay analyses of the morphological data. The strongest results of the bootstrap analysis are the monophyly of angiosperms, seen in 100% (more precisely 99.9%) of the bootstrap replicates, and, within the angiosperms, the association of Saururaceae and Piperaceae (99%). This contradicts the tree of Taylor & Hickey (1992), in which Saururaceae and Piperaceae are distantly separated. Next strongest is the link between angiosperms and Gnetales (95%). The monophyly of Gnetales is somewhat weaker (92%); examination of lower-frequency groupings indicates that this is because angiosperms are nested within Gnetales in some replicates, presumably due to features that they share with *Welwitschia* and *Gnetum* (reticulate venation, paracytic stomata, cellular embryogeny). Presumably, features of this sort are responsible for the position of angiosperms among Gnetales in some of the trees of Nixon et al. (1994). The Loconte & Stevenson (1990) arrangement of cycads, *Ginkgo*, and conifers occurs at a frequency of 79%. Except for Piperales, groupings within angiosperms that were seen in Donoghue & Doyle (1989a) appear at much lower frequencies, the strongest being the eudicots (43%).

The bootstrap results also bear on the rooting problem, although only indirectly. Insights come

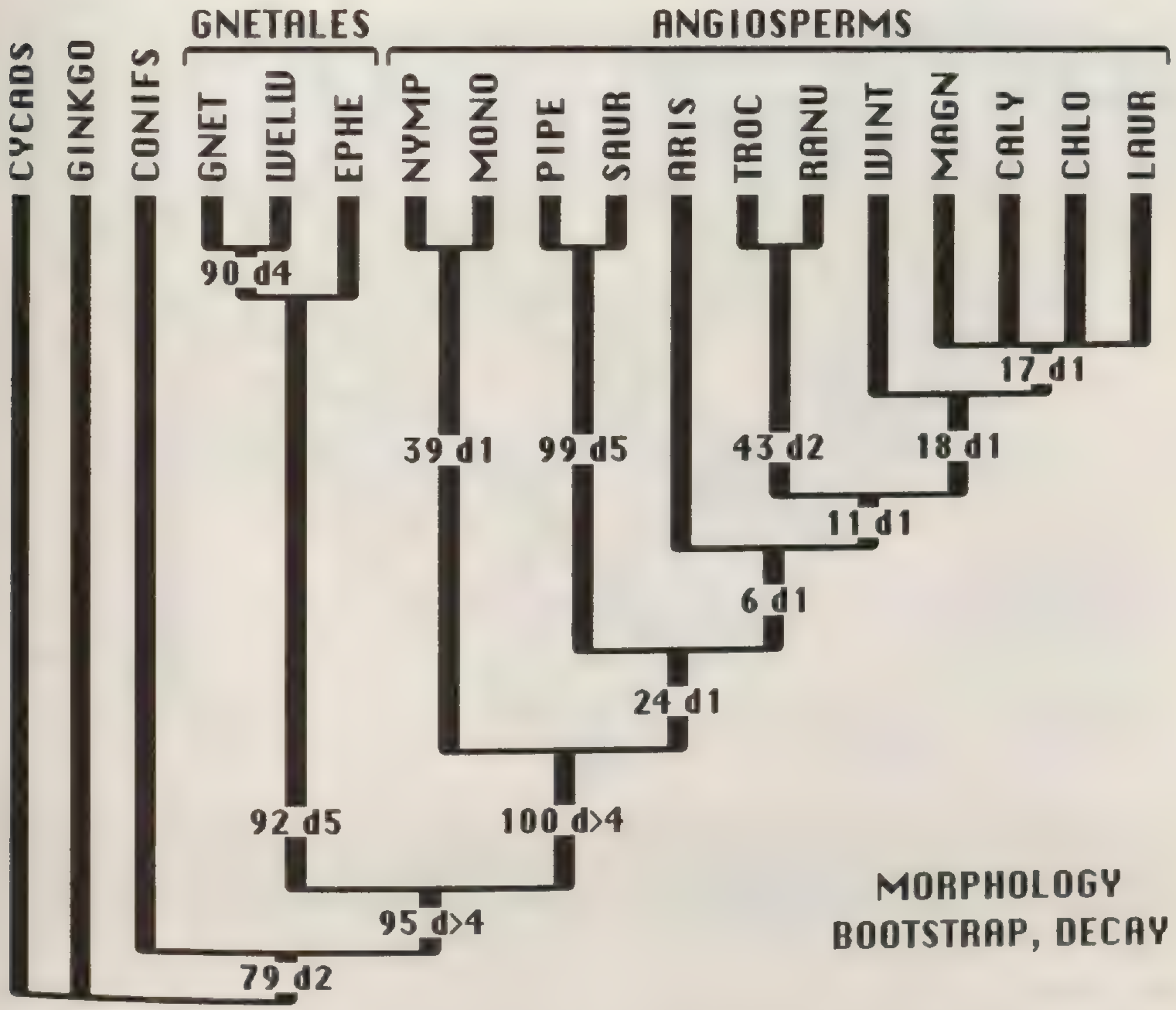

FIGURE 11. Results of bootstrap and decay analyses of the morphological data set. The first number indicates the percentage of bootstrap replicates in which each clade is found; the second number (d1, etc.) indicates how many steps longer trees must be before some are found in which the clade no longer occurs (decays). The search of five-off trees was incomplete; clades that had not decayed in that search are labeled d > 4, because we cannot rule out the possibility that they do decay in "islands" of five-off trees that were not discovered. Abbreviations as in Figure 8.

from examining the frequency of angiosperm clades containing all but one or two taxa, which imply that the taxa not included are basal, without specifying their exact arrangement. As expected, groupings implying that Nymphaeales and monocots are basal are most frequent, but at only 24%, followed by Nymphaeales alone at 17%, and Magnoliales at 11%. These results again illustrate the instability of the root, while favoring the same alternatives inferred from the primary analysis.

The decay numbers in Figure 11 refer to the number of steps that must be added (how many steps longer trees must be) before the group in question no longer forms a clade; e.g., "d2" indicates that it is present in all one-off trees but "decays" in some two-off trees (152 steps). In the consensus of one-off trees, the only clades remaining within angiosperms are Piperales (Piperaceae and Saururaceae) and eudicots (Ranunculidae and Trochodendrales). This result reflects the unstable position of the root; the one-off trees include not only those rooted among paleoherbs and next to Magnoliales, but also some rooted next to eudicots, next to paleoherbs as a group (as in the nine-angiosperm analysis: Fig. 5), and next to woody magnoliids as a group. It also illustrates the fact that strict consensus trees may underestimate the amount of structure in the data: if a single taxon (or the root) "jumps" from one clade to another, the intervening groups collapse to a polychotomy, even though their other members maintain the same arrangement. Eudicots decay in two-off trees, leaving only Piperales. The arrangement of cycads, *Ginkgo*, and conifers decays in two steps, and the relationship between *Welwitschia* and *Gnetum* in four. However, angiosperms, Gnetales, the relationship between them, and Piperales are still intact in the four-off trees. Five-off trees were not searched exhaustively because of time and memory limitations, but both Piperales and Gnetales decayed in

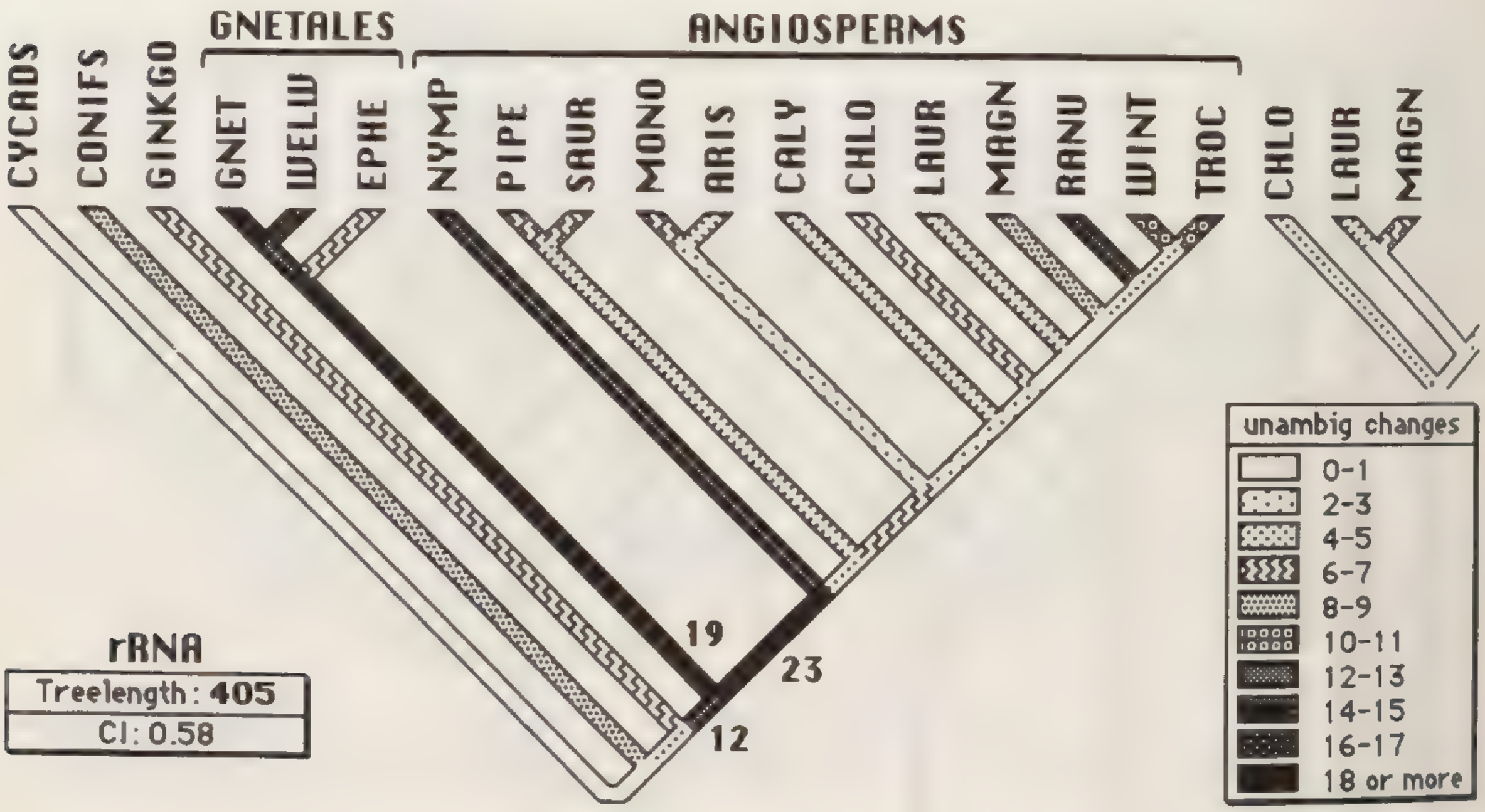

FIGURE 12. The two most parsimonious trees found in analysis of the rRNA data set, showing the number of unambiguous changes supporting each clade. Abbreviations as in Figure 8.

several incomplete searches at this length. The decay of Gnetales reflects trees in which angiosperms are nested within the group (cf. Nixon et al., 1994), since trees found by forcing angiosperms together with *Welwitschia* and *Gnetum* are of this length (155 steps). Angiosperms and anthophytes remain as clades in all five-off trees found, but because we cannot be certain that they do not decay in "islands" of trees that were not searched, they are labeled d > 4. This decay order closely parallels the relative strength of clades inferred from bootstrap analysis.

RESULTS OF rRNA ANALYSES

Analysis of the rRNA data yields two most parsimonious trees of 405 steps (Fig. 12), differing only in the relationship of Magnoliales and core Laurales. These trees are generally consistent with those derived from the whole rRNA data set (cf. Fig. 8), except in the exact arrangement of eudicots and woody magnoliids. The consistency index is 0.58, the same as in the morphological analysis; the retention index is 0.66. Based on this comparison, there is no reason to assume a priori that the rRNA data are any more or less reliable than the morphological data, although strong conclusions on relative consistency would be unwarranted because of differing amounts of missing data.

The arrangement of cycads, conifers, and *Ginkgo* differs from that derived from morphology, in that the group closest to anthophytes is *Ginkgo* rather than conifers. Angiosperms and Gnetales are united by at least 12 characters. However, it should be noted that conclusions on angiosperm outgroups are a function of the rooting of seed plants as a whole. When the whole rRNA data set is rooted with *Equisetum* and *Psilotum* (as in Hamby & Zimmer, 1992), it is only two steps less parsimonious to associate angiosperms with a clade consisting of *Ginkgo*, cycads, and conifers, rather than with Gnetales. The figure of 12 synapomorphies holds if seed plants are rooted somewhere among cycads, conifers, and *Ginkgo*, which we consider most likely. Certainly this is more consistent with analyses that include fossils (Crane, 1985; Doyle & Donoghue, 1986, 1992) and with the stratigraphic record; cycads, conifers, and ginkgos appear in the Late Carboniferous or Permian, but Gnetales (or forms on the line leading to them) are not known before the Late Triassic (Crane, 1988; Doyle & Donoghue, 1993).

Angiosperms themselves are united by at least 23 characters. As with previous rRNA analyses (Hamby & Zimmer, 1992), they are rooted among the paleoherbs: Nymphaeales are the sister group of other angiosperms, followed by Piperales, then Aristolochiaceae plus monocots. The fact that there are 13 unambiguous changes uniting Nymphaeales and four more between the nodes where Nymphaeales and Piperales are attached may raise suspicion that this rooting is an artifact of long branch attraction between Nymphaeales and the outgroups. However, at least two considerations argue

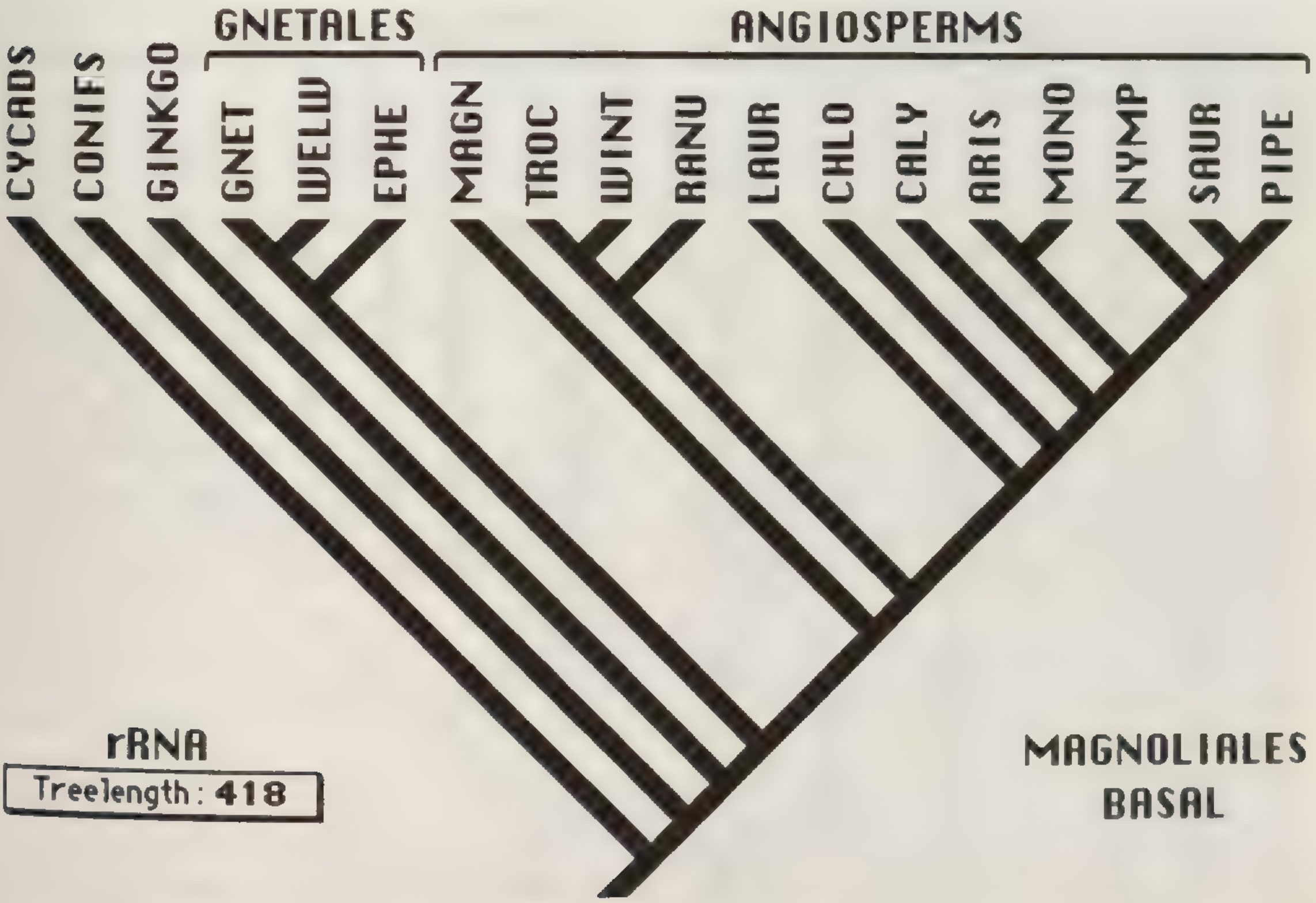

FIGURE 13. Representative tree found with the rRNA data set when Magnoliales are forced to the base of angiosperms and paleoherbs are forced together as a clade, as in most parsimonious trees of Donoghue & Doyle (1989a) and Figure 10 above. This tree is 13 steps longer than the most parsimonious trees. Abbreviations as in Figure 8.

against this. First, trees with the positions of Piperales and Nymphaeales reversed, which are equally "paleoherb-rooted," are only two steps longer, even though Piperales are a relatively short branch. Second, reanalysis of the data set without Nymphaeales results in two trees otherwise identical to those in Figure 12, with Piperales basal.

Experiments in which alternative groups were forced together with the constraints option in PAUP also support the view that the conflicts between the rRNA and morphological results are not serious. For example, Winteraceae are interpolated between Ranunculidae and Trochodendrales in the rRNA trees, breaking up the eudicots, but forcing the eudicots together adds only two steps (if Magnoliales are linked with core Laurales). On the other hand, whereas trees rooted next to Magnoliales and among paleoherbs are almost equally parsimonious in terms of morphology, the magnolialian rooting is much less parsimonious in terms of rRNA data. When Magnoliales are forced to the base of the angiosperms, the resulting trees are nine steps longer than the shortest trees (414 steps). Furthermore, these trees are not closely analogous to magnolialian-rooted trees based on morphology, because paleoherb groups are interpolated in various arrangements between Magnoliales and other woody magnoliids and eudicots. These are essentially paleoherb-rooted trees with Magnoliales alone pulled to the base. A more analogous tree, obtained by rerooting one of the most parsimonious angiosperm networks on the line leading to Magnoliales (Fig. 13), is 13 steps longer than the most parsimonious trees.

Experiments of this kind fail to support other current hypotheses on the rooting of angiosperms. Trees with Chloranthaceae forced to the base of the angiosperms (cf. Taylor & Hickey, 1992) are 10 steps longer than the shortest trees, roughly the same deficit seen when Magnoliales are basal. Trees with Calycanthaceae basal in angiosperms (cf. Loconte & Stevenson, 1991) are eight steps longer. As when Magnoliales are forced to the base, paleoherbs are interpolated between the basal group and other woody magnoliids and eudicots. The shortest trees obtained by rerooting the most parsimonious angiosperm networks on the line leading to Chloranthaceae and Calycanthaceae are 11 and nine steps longer, respectively; the latter tree is relatively parsimonious because paleoherbs are a next-most-basal clade. Trees with eudicots as the sister group of other (monosulcate) angiosperms,

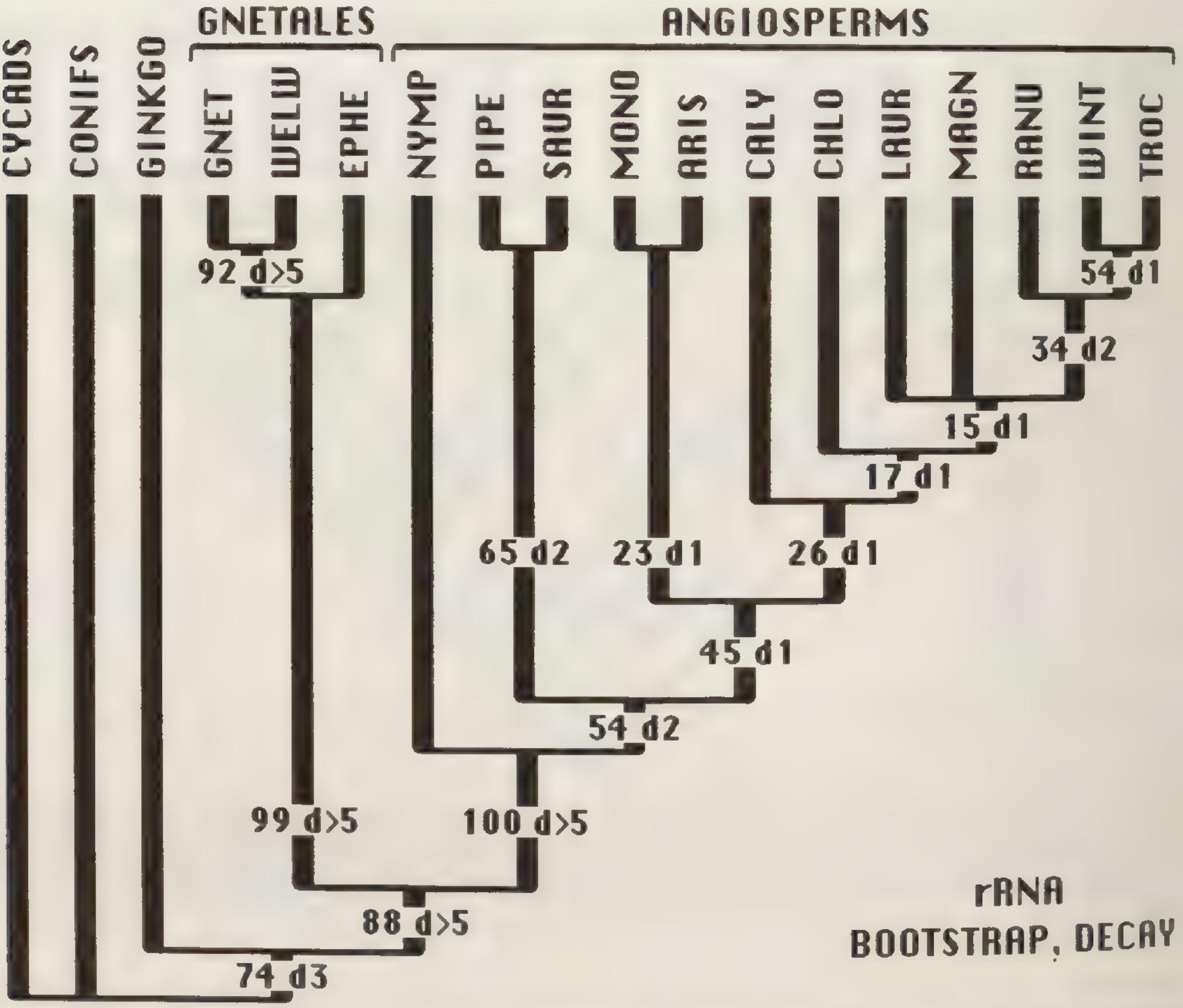

FIGURE 14. Results of bootstrap and decay analyses of the rRNA data set (see Fig. 11 for explanation). Abbreviations as in Figure 8.

analogous to trees based on *rbc*L data (Les et al., 1991; Chase et al., 1993; Qiu et al., 1993), are 14 steps longer than the shortest trees.

Results of bootstrap analysis of the rRNA data (Fig. 14) also complement those based on morphology. Again, the monophyly of the angiosperms is very strongly supported (99.997%). The link between angiosperms and Gnetales is weaker (88%), but the monophyly of Gnetales is stronger (99%). This result supports the view that the weaker morphological support for Gnetales is due strictly to morphological convergences between the subgroup consisting of *Welwitschia* and *Gnetum* and angiosperms, and it argues against trees in which angiosperms are derived from (nested within) Gnetales (Nixon et al., 1994).

It may be objected that molecular evidence for angiosperm monophyly applies only to living groups, leaving open the possibility that different "angiosperm" lines were derived polyphyletically from different fossil "gymnosperm" lines. However, this objection is valid only if all angiosperms and their fossil relatives are more closely related to each other than they are to any living gymnosperm group, not if some angiosperm line is more closely related to any living gymnosperm group—such as Gnetales, as assumed by most polyphyleticists. For example, if some angiosperms were related to *Cavtonia* and others to Gnetales, and if molecular data gave the correct relationships among living taxa, angiosperms would form one branch associated with Gnetales and another located one or more nodes below, not a clade.

Within angiosperms, Piperales are less well supported than they were with morphology (65%), but they are the strongest grouping, again contrary to Taylor & Hickey (1992). On the other hand, none of the rRNA links among angiosperms that conflicted with the morphological results are very strong. The grouping of Winteraceae and Trochodendrales, which breaks up the eudicots, appears at a frequency of only 54%. Although the connection between monocots and Aristolochiaceae is weak (23%), monocots are linked with Nym-

phaeales in only a negligible 1% of the bootstrap replicates. This may be another case where the rRNA data favor one alternative out of two that are almost equally parsimonious in terms of morphology; it requires only one extra step to associate monocots and Aristolochiaceae in the morphological analysis. The hypothesis that Aristolochiaceae are the sister group of monocots may be more plausible if Dioscoreales are basal in monocots, rather than alismids.

The rooting problem can again be addressed by examining the frequency of clades containing all but one or two angiosperm taxa. All higher-frequency groupings of this sort imply that one or another combination of paleoherb groups is basal: Nymphaeales in 54% of the bootstrap replicates, Nymphaeales and Piperales in 45%, Nymphaeales and monocots in 25%, Piperales in 22%, etc. In contrast, although Magnoliales were basal in 11% of the morphological replicates, they are basal in only 0.4% of the rRNA replicates. In other words, there is essentially no molecular "signal" in favor of the view that Magnoliales are basal angiosperms. This analysis also fails to support the concept that Calycanthaceae (Loconte & Stevenson, 1991) or Chloranthaceae (Taylor & Hickey, 1992) are basal: the corresponding groupings are observed at frequencies of less than 0.2%.

In the decay analysis (Fig. 14), Piperales and the group consisting of Winteraceae, Ranunculidae, and Trochodendrales are the only angiosperm clades left in the consensus of one-off trees. Both of these groups decay in two-off trees. The arrangement of cycads, conifers, and *Ginkgo* breaks down in three steps, but angiosperms, Gnetales, the relationship between them, and the association of *Welwitschia* and *Gnetum* are still intact in five-off trees, beyond which the analysis was abandoned. This decay order is generally consistent with the relative strength of clades inferred from the bootstrap analysis, although less precisely than with the morphological data.

RESULTS OF COMBINED ANALYSES

Analysis of the combined data set (Fig. 15) yields only one tree of 563 steps. The consistency index is 0.57, which is almost identical to that in the two separate analyses (0.58); the retention index is 0.67. This refutes one possible argument against combining morphological and molecular data, namely that adding two homoplastic data sets should only result in more total noise.

Examination of Figure 15 and alternative trees demonstrates graphically the complementarity of the two data sets. In non-angiospermous groups, the Loconte & Stevenson (1990) arrangement is favored. However, the conifer–anthophyte link is unequivocally supported by only six characters, and trees with conifers and *Ginkgo* reversed are only one step longer. The strong links inferred from both component data sets are seen among Gnetales (united by at least 26 characters), among angiosperms (40 characters), and between angiosperms and Gnetales (15 characters).

As expected from the ambiguity of the morphological results and the relative strength of the rRNA results, angiosperms are rooted among the paleoherbs, with Nymphaeales basal. Trees with Magnoliales forced to the base of the angiosperms are 13 steps longer than the shortest tree; trees with Chloranthaceae and Calycanthaceae basal are 14 and 15 steps longer, respectively.

Despite the much greater number of rRNA characters, other results are more consistent with the morphological analysis, in keeping with the expectation that even a few morphological characters can be decisive when molecular data are ambiguous. Laurales and Magnoliales form a monophyletic group, as in the morphological trees, rather than a paraphyletic grade, as in the rRNA trees. Monocots are interpolated between Nymphaeales and Piperales, although it costs only one extra step to link them with Aristolochiaceae, as in the rRNA analysis. Most significantly, Ranunculidae and Trochodendrales form a eudicot clade—Winteraceae are dissociated from Trochodendrales and are instead the sister group of Laurales and Magnoliales.

The general result of the bootstrap analysis (Fig. 16) is that the two data sets tend to reinforce each other in cases where they were congruent. Angiosperms (100%), Gnetales (100%), Piperales (99%), and *Welwitschia* plus *Gnetum* (98%) form clades at bootstrap frequencies similar to or higher than those in the separate analyses. Angiosperms and Gnetales are united at the 98% level, rather than 95% in the morphological analysis and 88% in the rRNA analysis. This again belies the fear that conflicting patterns of homoplasy will simply lower overall resolution, and it suggests instead that both analyses are detecting the same real phylogenetic signal. Conversely, basal seed plant relationships, which conflicted but were weakly supported in both analyses, are less resolved: conifers and anthophytes are linked at a frequency of only 54%, rather than 79% in the morphological analysis.

A more subtle effect is that the two data sets also seem to reinforce each other in one case where the most parsimonious trees derived from them

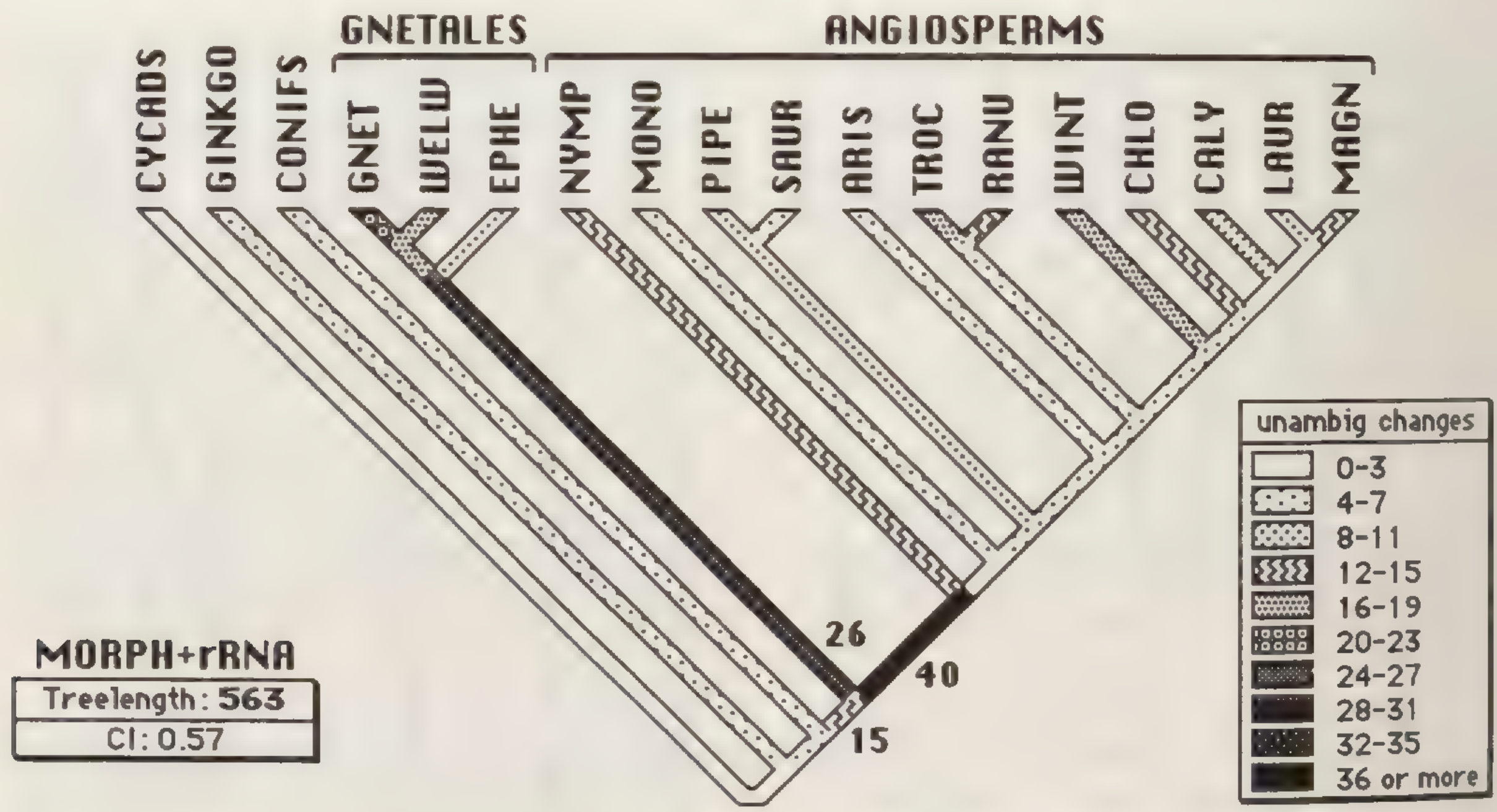

FIGURE 15. Single most parsimonious tree found in analysis of the combined morphological and rRNA data set, showing the number of unambiguous changes supporting each clade. Abbreviations as in Figure 8.

were *not* congruent. This involves the link between the two eudicot taxa, which is seen in 50% of the replicates in the combined analysis, rather than 43% in the morphological analysis and only 12% in the molecular analysis. We suspect that this reflects the existence of "minority" rRNA characters that support the eudicots (also supported by *rbc*L data: Chase et al., 1993). Once Winteraceae are forced outside eudicots by the morphological characters, these molecular characters reinforce those from morphology. The existence of such effects is a general argument for combining data sets (Barrett et al., 1991).

As in the rRNA analysis, the relative support for clades inferred from the decay analysis (Fig. 16) roughly parallels the bootstrap results. All the stronger clades decay more slowly than they did in either individual analysis, in keeping with the larger total number of characters. Eudicots appear to be more robust than implied by the bootstrap; they do not decay until four step less parsimonious trees. All groups retained in the four-off trees are still present in eight-off trees, beyond which the analysis was abandoned.

CONCLUSIONS

These exercises clearly show the utility of combining molecular and morphological data sets as well as analyzing them separately. This procedure has the potential of resolving conflicts between data sets even when one is much larger, presumably because there are minority characters in each data set that reflect true historical relationships (Barrett et al., 1991).

The strongest results of these analyses are that angiosperms, Gnetales, and Piperales (Piperaceae plus Saururaceae, but not Chloranthaceae) are monophyletic groups, and that Gnetales are the closest living relatives of angiosperms. We suggest that polyphyly of angiosperms can be set aside and other reasons examined for lack of progress in understanding the origin of the group (cf. Donoghue & Doyle, 1991). In contrast, relationships among cycads, conifers, *Ginkgo*, and anthophytes appear to be quite unresolved on present data, even when fossil taxa are considered (Doyle & Donoghue, 1992).

The potentially most significant result of this exercise concerns the rooting of the angiosperms. There appears to be essentially no rRNA support for the conclusion derived from morphology that Magnoliales are basal angiosperms, and a magnolialian rooting is increasingly ambiguous in terms of morphological data. Since there are still apparent conflicts with other molecular data sets, it would be premature to consider the paleoherb rooting established. However, our own preliminary experiments in combining morphological, rRNA, and *rbc*L data also give a paleoherb rooting, specifically between monocots and dicots. These analyses are not strictly comparable to the analyses presented above, since so far we have only used single exemplar species in the *rbc*L data set to represent

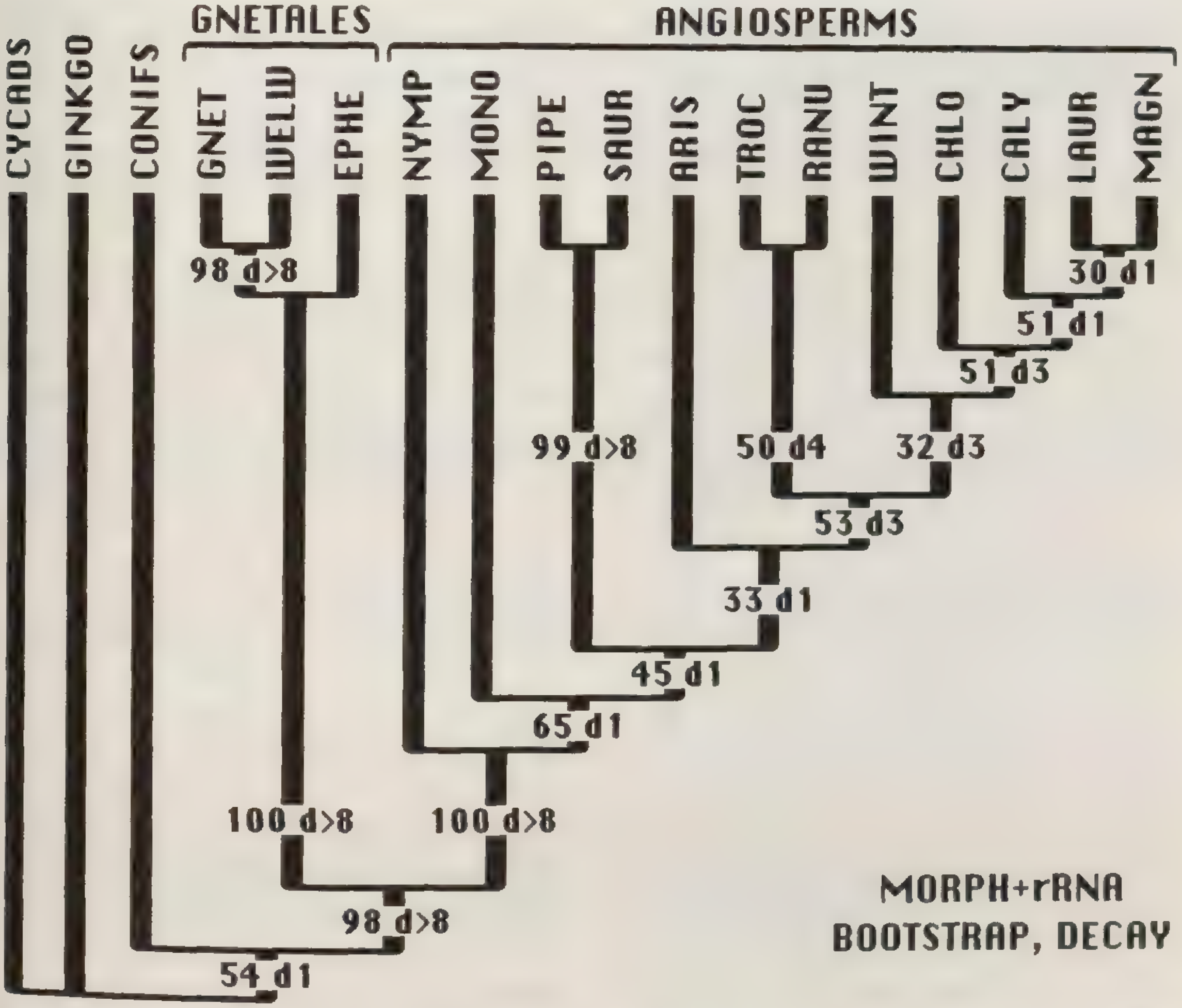

FIGURE 16. Results of bootstrap and decay analyses of the combined morphological and rRNA data set (see Fig. 11 for explanation). Abbreviations as in Figure 8.

presumed clades. Still, it appears that the *rbc*L data do not support some different arrangement so strongly that they overwhelm the other data, even though there are more potentially informative *rbc*L characters than rRNA characters.

Until the disagreements among molecular data sets are resolved, paleoherbs clearly deserve as much attention from botanists as has been paid to woody magnoliids. To discourage potential misconceptions, we should clarify what a paleoherb rooting would say about primitive conditions (cf. Taylor & Hickey, 1992). Although our trees imply that the first angiosperms would be at least semiherbaceous, the aquatic habit and complete lack of secondary growth in Nymphaeales and monocots may be autapomorphies of these groups. Leaves would have more or less palmate venation and anomocytic stomates; contrary to Doyle & Donoghue (1986), the paracytic stomates of woody magnoliids would be a convergence with Bennettitales. The fact that Piperales are near-basal might seem to support the view that small, crowded flowers with orthotropous ovules and no perianth are primitive (Burger, 1977; Taylor & Hickey, 1990, 1992). However, if taxa are arranged as in Figures 9, 12, or 15, it is more parsimonious to assume that angiosperms originally had flowers like those of Cabombaceae, *Lactoris*, *Saruma* (Aristolochiaceae), and monocots, with one or two cycles of three perianth parts, a trimerous androecium and gynoecium, and anatropous ovules. The syncarpous gynoecium of Nymphaeaceae and the tubular calyx and inferior ovary of most Aristolochiaceae would be autapomorphies, although the laminar placentation of Nymphaeales as a whole might be primitive. Stamens would be differentiated into filament and anther, not laminar as in woody magnoliids. The basal position of Nymphaeales and Piperales raises the intriguing possibility that the presence of both endosperm and perisperm in seeds of these orders is a primitive transitional state, not derived as usually assumed (D. Haig, pers. comm.). The conclusion that Gnetales are the closest modern relatives of angiosperms permits a wide range of floral prototypes, depending on how fossil taxa

are arranged, from showy flowers, as in Bennettitales, to simple ones, as in Gnetales.

As stressed by Taylor & Hickey (1990), a (semi)herbaceous habit might help explain why the earliest phases of angiosperm evolution and angiosperm precursors have been overlooked in the fossil record. However, this does not mean that the search for paleobotanical data is hopeless: paleoherblike precursors might be represented in the pollen, fruit, or seed records, and vegetative remains might be preserved in special facies, like *Acaciaephyllum* (a probable monocot) and *Nelumbites* (an aquatic with peltate leaves) in the Early Cretaceous (Doyle & Hickey, 1976). Pollen of Nymphaeales and Piperales is probably apomorphic in being very large and very small, respectively, but the two groups are similar in having columellar rather than granular structure (although the columellae are hard to recognize without TEM: cf. Osborn et al., 1991) and a complete tectum. If this is the basic pollen type for angiosperms, it would be difficult but not impossible to recognize in the dispersed state.

The apparent conflicts among present molecular data sets raise the possibility that molecular data are simply incapable of resolving the rooting problem (cf. Donoghue et al., 1989), although methods of factoring out the effects of long branch attraction (as discussed by Albert et al., 1994) or discovery of genome rearrangements or duplications that occurred early in the angiosperm radiation (cf. Iwabe et al., 1989; Raubeson & Jansen, 1992) might permit firmer inferences. It is possible that significant progress on the origin of angiosperms will require recognition of fossil forms on the long branch leading to the group. Potential examples include *Phyllites* (Seward, 1904), a Jurassic leaf with paleoherblike palmate venation; Triassic Crinopolles pollen (Cornet, 1989a), with monocotlike sculpture; and the still-enigmatic Triassic fossil *Sanmiguelia* (Cornet, 1986, 1989b; Doyle & Hotton, 1991; Doyle & Donoghue, 1993). Better evidence on the morphology of *Caytonia* and glossopterids—whether or not they have anthophyte states in currently unknown characters, as required in trees where they are linked with angiosperms—could also have a decisive effect in choosing among alternative angiosperm relationships. Better reconstructions of primitive members or stem-relatives of Bennettitales and Gnetales could clarify whether flowers are indeed a synapomorphy of anthophytes or arose independently in each anthophyte line, a possibility raised by the existence of less flowerlike Late Triassic–Early Jurassic reproductive structures related to these groups (*Westersheimia*, *Vardekloeftia*, *Dechellyia*, *Piroconites*: Crane, 1988; van Konijnenburg-van Cittert, 1992).

Another possibility is that evidence on the genetic control of floral development in angiosperms and Gnetales might indirectly distinguish among alternative arrangements of anthophyte groups by impinging upon associated scenarios of floral evolution (Doyle, 1993). If angiosperms are basal in anthophytes and flowers of both angiosperms and Gnetales are derived from a flowerlike prototype (a "euanthial" scenario, as in Doyle & Donoghue, 1986), the outer integument of Gnetales should be homologous with the perianth of angiosperms, and homologs of genes such as *apetala 2* that specify perianth development in *Arabidopsis* (Coen & Meyerowitz, 1991) might be active during development of the gnetalian outer integument. On the other hand, trees that link angiosperms directly with Gnetales and place groups like Chloranthaceae and/or Piperales at the base of the angiosperms (Taylor & Hickey, 1992; Nixon et al., 1994) suggest that typical angiosperm flowers may actually be pseudanthia, with carpels derived from bracts and axillary units. If so, the outer integument of Gnetales might be homologous with the outer integument of angiosperms, and its development might be associated with the activity of homologs of genes that control development of the angiosperm outer integument (Robinson-Beers et al., 1992).

Literature Cited

Albert, V. A., A. Backlund, K. Bremer, M. W. Chase, J. R. Manhart, B. D. Mishler & K. C. Nixon. 1994. Functional constraints and *rbc*L evidence for land plant phylogeny. Ann. Missouri Bot. Gard. 81: 534–567.

Barrett, M., M. J. Donoghue & E. Sober. 1991. Against consensus. Syst. Zool. 40: 486–493.

Beck, C. B., R. Schmid & G. W. Rothwell. 1982. Stelar morphology and the primary vascular system of seed plants. Bot. Rev. 48: 691–815.

Behnke, H.-D. 1988. Sieve-element plastids, phloem protein, and evolution of flowering plants: III. Magnoliidae. Taxon 37: 699–732.

Bornstein, A. J. 1989. Taxonomic studies in the Piperaceae—I. The pedicellate pipers of Mexico and Central America (*Piper* subg. *Arctottonia*). J. Arnold Arbor. 70: 1–55.

Bremer, K. 1988. The limits of amino acid sequence data in angiosperm phylogenetic reconstruction. Evolution 42: 795–803.

Bull, J. J., J. P. Huelsenbeck, C. W. Cunningham, D. L. Swofford & P. J. Waddell. 1993. Partitioning and combining data in phylogenetic analysis. Syst. Zool. 42: 384–397.

Burger, W. C. 1977. The Piperales and the monocots. Alternative hypotheses for the origin of monocotyledonous flowers. Bot. Rev. 43: 345–393.

———. 1981. Heresy revived: The monocot theory of angiosperm origin. Evol. Theory 5: 189–225.

CARLQUIST, S. 1990. Wood anatomy and relationships of Lactoridaceae. Amer. J. Bot. 77: 1498–1504.

CARPENTER, J. M. 1992. Random cladistics. Cladistics 8: 147–153.

CHASE, M. W. & 41 OTHERS. 1993. Phylogenetics of seed plants: An analysis of nucleotide sequences from the plastid gene *rbc*L. Ann. Missouri Bot. Gard. 80: 528–580.

CHLONOVA, A. F. & T. D. SUROVA. 1988. Pollen wall ultrastructure of *Clavatipollenites incisus* Chlonova and two modern species of *Ascarina* (Chloranthaceae). Pollen & Spores 30: 29–44.

COEN, E. S. & E. M. MEYEROWITZ. 1991. The war of the whorls: Genetic interactions controlling flower development. Nature 353: 31–37.

CORNET, B. 1986. The leaf venation and reproductive structures of a Late Triassic angiosperm, *Sanmiguelia lewisii*. Evol. Theory 7: 231–309.

———. 1989a. Late Triassic angiosperm-like pollen from the Richmond rift basin of Virginia, U.S.A. Palaeontographica, Abt. B 213: 37–87.

———. 1989b. The reproductive morphology and biology of *Sanmiguelia lewisii*, and its bearing on angiosperm evolution in the Late Triassic. Evol. Trends Pl. 3: 25–51.

CRANE, P. R. 1985. Phylogenetic analysis of seed plants and the origin of angiosperms. Ann. Missouri Bot. Gard. 72: 716–793.

———. 1988. Major clades and relationships in the "higher" gymnosperms. Pp. 218–272 *in* C. B. Beck (editor), Origin and Evolution of Gymnosperms. Columbia Univ. Press, New York.

CRONQUIST, A. 1981. An Integrated System of Classification of Flowering Plants. Columbia Univ. Press, New York.

———. 1988. The Evolution and Classification of Flowering Plants, 2nd ed. New York Botanical Garden, Bronx, New York.

DAVIS, G. L. 1966. Systematic Embryology of the Angiosperms. John Wiley & Sons, New York.

DONOGHUE, M. J. 1994. Progress and prospects in reconstructing plant phylogeny. Ann. Missouri Bot. Gard. 81: 405–418.

——— & J. A. DOYLE. 1989a. Phylogenetic analysis of angiosperms and the relationships of Hamamelidae. Pp. 17 45 *in* P. R. Crane & S. Blackmore (editors), Evolution, Systematics, and Fossil History of the Hamamelidae, vol. 1. Clarendon Press, Oxford.

——— & J. A. DOYLE. 1989b. Phylogenetic studies of seed plants and angiosperms based on morphological characters. Pp. 181–193 *in* B. Fernholm, K. Bremer & H. Jörnvall (editors), The Hierarchy of Life. Elsevier, Amsterdam.

——— & ———. 1991. Angiosperm monophyly. Trends Ecol. Evol. 6: 407.

——— & M. J. SANDERSON. 1992. The suitability of molecular and morphological evidence in reconstructing plant phylogeny. Pp. 340–368 *in* P. S. Soltis, D. E. Soltis & J. J. Doyle (editors), Molecular Systematics of Plants. Chapman & Hall, New York.

——— & S. M. SCHEINER. 1992. The evolution of endosperm: A phylogenetic account. Pp. 356-389 *in* R. Wyatt (editor), Ecology and Evolution of Plant Reproduction: New Approaches. Chapman & Hall, New York.

———, R. G. OLMSTEAD, J. F. SMITH & J. D. PALMER. 1992. Phylogenetic relationships of Dipsacales based on *rbc*L sequences. Ann. Missouri Bot. Gard. 79: 333–345.

———, J. A. DOYLE, J. GAUTHIER, A. G. KLUGE & T. ROWE. 1989. The importance of fossils in phylogeny reconstruction. Annual Rev. Ecol. Syst. 20: 431–460.

DOYLE, J. A. 1993. Cladistic and paleobotanical perspectives on the origin of angiosperm organs. J. Cell. Biochem., Suppl. 17B: 8.

——— & M. J. DONOGHUE. 1986. Seed plant phylogeny and the origin of angiosperms: An experimental cladistic approach. Bot. Rev. 52: 321–431.

——— & ———. 1987. The importance of fossils in elucidating seed plant phylogeny and macroevolution. Rev. Palaeobot. Palynol. 50: 63–95.

——— & ———. 1990. Reexamination of seed plant and angiosperm relationships. Amer. J. Bot. 77(6, Suppl.): 84.

——— & ———. 1992. Fossils and seed plant phylogeny reanalyzed. Brittonia 44: 89–106.

——— & ———. 1993. Phylogenies and angiosperm diversification. Paleobiology 19: 141–167.

——— & L. J. HICKEY. 1976. Pollen and leaves from the mid-Cretaceous Potomac Group and their bearing on early angiosperm evolution. Pp. 139–206 *in* C. B. Beck (editor), Origin and Early Evolution of Angiosperms. Columbia Univ. Press, New York.

——— & C. L. HOTTON. 1991. Diversification of early angiosperm pollen in a cladistic context. Pp. 169–195 *in* S. Blackmore & S. H. Barnes (editors), Pollen and Spores: Patterns of Diversification. Clarendon Press, Oxford.

DUVALL, M. R., M. T. CLEGG, M. W. CHASE, W. D. CLARK, W. J. KRESS, H. G. HILLS, L. E. EGUIARTE, J. F. SMITH, B. S. GAUT, E. A. ZIMMER & G. H. LEARN, JR. 1993. Phylogenetic hypotheses for the monocotyledons constructed from *rbc*L sequence data. Ann. Missouri Bot. Gard. 80: 607–619.

EHRENDORFER, F. 1976. Evolutionary significance of chromosomal differentiation patterns in gymnosperms and primitive angiosperms. Pp. 220 240 *in* C. B. Beck (editor), Origin and Early Evolution of Angiosperms. Columbia Univ. Press, New York.

ENDRESS, P. K. 1983. Dispersal and distribution in some small archaic relic angiosperm families (Austrobaileyaceae, Eupomatiaceae, Himantandraceae, Idiospermoideae Calycanthaceae). Sonderb. Naturwiss. Vereins Hamburg 7: 201 217.

———. 1987. The Chloranthaceae: Reproductive structures and phylogenetic position. Bot. Jahrb. Syst. 109: 153–226.

FELSENSTEIN, J. 1978. Cases in which parsimony or compatibility methods will be positively misleading. Syst. Zool. 27: 401–410.

———. 1985. Confidence limits on phylogenies: An approach using the bootstrap. Evolution 39: 783–791.

——— & H. KISHINO. 1993. Is there something wrong with the bootstrap on phylogenies? A reply to Hillis and Bull. Syst. Zool. 42: 193–200.

FRIEDMAN, W. E. 1990. Sexual reproduction in *Ephedra nevadensis* (Ephedraceae): Further evidence of double fertilization in a nonflowering seed plant. Amer. J. Bot. 77: 1582–1598.

———. 1992. Evidence of a pre-angiosperm origin of endosperm: Implications for the evolution of flowering plants. Science 255: 336–339.

GABARAYEVA, N. I. 1991. Patterns of development in primitive angiosperm pollen. Pp. 257–268 *in* S. Blackmore & S. H. Barnes (editors), Pollen and Spores: Patterns of Diversification. Clarendon Press, Oxford.

GIBBS, R. D. 1957. The Mäule reaction, lignin, and the relationships between woody plants. Pp. 269–312 *in* K. V. Thimann (editor), The Physiology of Forest Trees. Ronald Press, New York.

GIFFORD, E. M. & A. S. FOSTER. 1989. Morphology and Evolution of Vascular Plants. W. H. Freeman, New York.

GILLESPIE, L. J. & J. W. NOWICKE. 1992. Systematic implications of pollen morphology in *Gnetum*. 8th Int. Palynol. Congr. (Aix-en-Provence) Abstr. 53.

GOLENBERG, E. M., D. E. GIANNASI, M. T. CLEGG, C. J. SMILEY, M. DURBIN, D. HENDERSON & G. ZURAWSKI. 1990. Chloroplast DNA sequence from a Miocene *Magnolia* species. Nature 344: 656–658.

HAMBY, R. K. & E. A. ZIMMER. 1992. Ribosomal RNA as a phylogenetic tool in plant systematics. Pp. 50–91 *in* P. S. Soltis, D. E. Soltis & J. J. Doyle (editors), Molecular Systematics of Plants. Chapman & Hall, New York.

HART, J. A. 1987. A cladistic analysis of conifers: Preliminary results. J. Arnold Arbor. 68: 269–307.

HASEBE, M., K. KOFUJI, M. ITO, M. KATO, K. IWATSUKI & K. UEDA. 1992. Phylogeny of gymnosperms inferred from *rbc*L gene sequences. Bot. Mag. (Tokyo) 105: 673–679.

HILLIS, D. M. 1987. Molecular versus morphological approaches to systematics. Annual Rev. Ecol. Syst. 18: 23–42.

——— & J. J. BULL. 1993. An empirical test of bootstrapping as a method for assessing confidence in phylogenetic analysis. Syst. Biol. 42: 182–192.

HUGHES, N. F. & A. B. MCDOUGALL. 1990. Barremian–Aptian angiospermid pollen records from southern England. Rev. Palaeobot. Palynol. 65: 145–151.

ITO, M. 1987. Phylogenetic systematics of the Nymphaeales. Bot. Mag. (Tokyo) 100: 17–35.

IWABE, N., K. KUMA, M. HASEGAWA, S. OSAWA & T. MIYATA. 1989. Evolutionary relationship of archaebacteria, eubacteria, and eukaryotes inferred from phylogenetic trees of duplicated genes. Proc. Natl. Acad. Sci. U.S.A. 86: 9355–9359.

KELLOGG, E. A. & C. S. CAMPBELL. 1987. Phylogenetic analyses of the Gramineae. Pp. 310–322 *in* T. R. Soderstrom, K. W. Hilu, C. S. Campbell & M. E. Barkworth (editors), Grass Systematics and Evolution. Smithsonian Institution, Washington, D.C.

KLUGE, A. J. 1989. A concern for evidence and a phylogenetic hypothesis of relationships among *Epicrates* (Boidae, Serpentes). Syst. Zool. 38: 7–25.

KRASSILOV, V. A. 1991. The origin of angiosperms: New and old problems. Trends Ecol. Evol. 6: 215–220.

LES, D. H., D. K. GARVIN & C. F. WIMPEE. 1991. Molecular evolutionary history of ancient aquatic angiosperms. Proc. Natl. Acad. Sci. U.S.A. 88: 10119–10123.

LE THOMAS, A. 1980–1981. Ultrastructural characters of the pollen grains of African Annonaceae and their significance for the phylogeny of primitive angiosperms. Pollen & Spores 22: 267–342, 23: 5–36.

LOCONTE, H. & D. W. STEVENSON. 1990. Cladistics of the Spermatophyta. Brittonia 42: 197–211.

——— & ———. 1991. Cladistics of the Magnoliidae. Cladistics 7: 267–296.

MADDISON, D. R. 1991. The discovery and importance of multiple islands of most-parsimonious trees. Syst. Zool. 40: 315–328.

———, M. RUVOLO & D. L. SWOFFORD. 1992. Geographic origins of human mitochondrial DNA: Phylogenetic evidence from control region sequences. Syst. Biol. 41: 111–124.

MADDISON, W. P. & D. R. MADDISON. 1992. MacClade: Analysis of Phylogeny and Character Evolution, Version 3. Sinauer Associates, Sunderland, Massachusetts.

METCALFE, C. R. 1987. Anatomy of the Dicotyledons, 2nd ed., vol. III. Magnoliales, Illiciales, and Laurales (*Sensu* Armen Takhtajan). Clarendon Press, Oxford.

MEYEN, S. V. 1984. Basic features of gymnosperm systematics and phylogeny as evidenced by the fossil record. Bot. Rev. 50: 1–112.

MISHLER, B. D. 1994. The cladistic analysis of molecular and morphological data. Amer. J. Phys. Anthropol. 94: 143–156.

MONEY, L. L., I. W. BAILEY & B. G. L. SWAMY. 1950. The morphology and relationships of the Monimiaceae. J. Arnold Arbor. 31: 372–404.

NIXON, K. C. & J. I. DAVIS. 1991. Polymorphic taxa, missing values and cladistic analysis. Cladistics 7: 233–241.

———, W. L. CREPET, D. STEVENSON & E. M. FRIIS. 1994. A reevaluation of seed plant phylogeny. Ann. Missouri Bot. Gard. 81: 484–533.

OSBORN, J. M., T. N. TAYLOR & E. L. SCHNEIDER. 1991. Pollen morphology and ultrastructure of the Cabombaceae: Correlations with pollination biology. Amer. J. Bot. 78: 1367–1378.

QIU, Y.-L., M. W. CHASE, D. H. LES & C. R. PARKS. 1993. Molecular phylogenetics of the Magnoliidae: Cladistic analyses of nucleotide sequences of the plastid gene *rbc*L. Ann. Missouri Bot. Gard. 80: 587–606.

QUEIROZ, A. DE. 1993. For consensus (sometimes). Syst. Biol. 42: 368–372.

RAUBESON, L. A. & R. K. JANSEN. 1992. Chloroplast DNA evidence on the ancient evolutionary split in vascular land plants. Science 255: 1697–1699.

ROBINSON-BEERS, K., R. E. PRUITT & C. S. GASSER. 1992. Ovule development in wild type Arabidopsis and two female-sterile mutants. Pl. Cell 4: 1237–1249.

ROTHWELL, G. W. 1982. New interpretations of the earliest conifers. Rev. Palaeobot. Palynol. 37: 7–28.

SANDERSON, M. J. & M. J. DONOGHUE. 1989. Patterns of variation in levels of homoplasy. Evolution 43: 1781–1795.

SERBET, R. & G. W. ROTHWELL. 1992. Characterizing the most primitive seed ferns: I. A reconstruction of *Elkinsia polymorpha*. Int. J. Pl. Sci. 153: 602–621.

SEWARD, A. C. 1904. Catalogue of Mesozoic Plants in the British Museum. The Jurassic Flora, Part 1. British Museum (Natural History), London.

STEVENSON, D. W. 1990. Morphology and systematics of the Cycadales. Mem. New York Bot. Gard. 57: 8–55.

SWOFFORD, D. L. 1991. PAUP: Phylogenetic Analysis

Using Parsimony, Version 3.0. Illinois Natural History Survey, Champaign, Illinois.

——— & W. P. MADDISON. 1987. Reconstructing ancestral states under Wagner parsimony. Math. Biosci. 87: 199–229.

TAKHTAJAN, A. L. 1969. Flowering Plants: Origin and Dispersal. Smithsonian Institution, Washington, D.C.

TAYLOR, D. W. & L. J. HICKEY. 1990. An Aptian plant with attached leaves and flowers: Implications for angiosperm origin. Science 247: 702–704.

——— & ———. 1992. Phylogenetic evidence for the herbaceous origin of angiosperms. Pl. Syst. Evol. 180: 137–156.

TROITSKY, A. V., YU. F. MELEKHOVETS, G. M. RAKHIMOVA, V. K. BOBROVA, K. M. VALIEJO-ROMAN & A. S. ANTONOV. 1991. Angiosperm origin and early stages of seed plant evolution deduced from rRNA sequence comparisons. J. Molec. Evol. 32: 253–261.

VAN CAMPO, M. & B. LUGARDON. 1973. Structure grenue infratectale de l'ectexine des pollens de quelques Gymnospermes et Angiospermes. Pollen & Spores 15: 171–187.

VAN KONIJNENBURG-VAN CITTERT, J. H. A. 1992. An enigmatic Liassic microsporophyll, yielding *Ephedripites* pollen. Rev. Palaeobot. Palynol. 71: 239–254.

VINK, W. 1988. Taxonomy in Winteraceae. Taxon 37: 691–698.

VOGEL, E. F. DE. 1980. Seedlings of Dicotyledons. Centre for Agricultural Publishing and Documentation, Wageningen.

WAKE, D. B. 1991. Homoplasy: The result of natural selection, or evidence of design limitations? Amer. Naturalist 138: 543–567.

WALKER, J. W. 1976. Evolutionary significance of the exine in the pollen of primitive angiosperms. Pp. 1112–1137 *in* I. K. Ferguson & J. Muller (editors), The Evolutionary Significance of the Exine. Academic Press, London.

WHEELER, W. C. 1990. Nucleic acid sequence phylogeny and random outgroups. Cladistics 6: 363–367.

ZAVADA, M. 1984. Angiosperm origins and evolution based on dispersed fossil pollen ultrastructure. Ann. Missouri Bot. Gard. 71: 444–463.

ZIMMER, E. A., R. K. HAMBY, M. L. ARNOLD, D. A. LEBLANC & E. C. THERIOT. 1989. Ribosomal RNA phylogenies and flowering plant evolution. Pp. 205–214 *in* B. Fernholm, K. Bremer & H. Jörnvall (editors), The Hierarchy of Life. Elsevier, Amsterdam.

APPENDIX.

MORPHOLOGICAL CHARACTERS. Character definitions and justification follow Doyle & Donoghue (1992) for characters 1–50 (except 48) and Donoghue & Doyle (1989a) for characters 57–82, unless otherwise indicated. Where the nine-angiosperm (fossil and extant) and 12-angiosperm (extant) data sets differ in definition of characters, definitions for the former analysis are given first.

1. Branching (0) apical, (1) axillary.
2. Axillary buds (0) single, (1) multiple.
3. Phyllotaxy (0) spiral, (1) opposite or whorled, (2) distichous.
4. Leaves (0) all dichotomous, (1) linear or dichotomous plus cataphylls, (2) simple pinnate plus cataphylls, (3) pinnately compound plus cataphylls, (4) palmately veined (actino- or acrodromous) plus cataphylls; extant analysis: (0) simple pinnate, (1) linear or dichotomous, (2) palmately veined. States 0 and 1 of Donoghue & Doyle (1989a) (elliptical or obovate, secondary veins at constant angle or lower angle at base, vs. ovate, basal secondaries crowded, at higher angle) are combined under simple pinnate; the only taxa with Donoghue & Doyle's state 1 are *Austrobaileya* and Calycanthaceae, only one of which appears in each of the present data sets.
5. Rachis (0) bifurcate, (1) simple.
6. Laminar venation (0) open, (1) reticulate.
7. Laminar vein orders (0) one, (1) two or more.
8. Guard cell poles (0) raised, (1) level with aperture.
9. Stomates (0) anomocytic, (1) mostly paracytic, (2) laterocytic or variable, (3) tetracytic. Core Laurales were scored as unknown in Donoghue & Doyle (1989a), but the basal state with the ingroup relationships assumed here (Fig. 8) is paracytic.
10. Apical meristem (0) without tunica, (1) with tunica.
11. Stele (0) protostele, (1) eustele with external secondary xylem only, (2) eustele with internal secondary xylem.
12. Primary xylem (0) mesarch, (1) endarch.
13. Nodes (0) unilacunar, one-trace, (1) multilacunar (more than three traces from separate primary xylem bundles, arcuate in petiole), (2) unilacunar, two-trace, (3) trilacunar. The medullosan condition (many traces derived from one solid mass or several arcs of primary xylem, scattered in petiole) was treated as a separate state in Doyle & Donoghue (1992), but because it is uninformative we have eliminated the state and rescored medullosans as unknown; this change should have no effect on the results. Trochodendrales are scored as trilacunar because *Trochodendron* is polymorphic but *Tetracentron* is trilacunar (Cronquist, 1981). Core Laurales have various numbers of traces, but these are usually formed by the splitting of two traces (Money et al., 1950; Beck et al., 1982), so we interpret the group as basically two-trace.
14. Primary xylem (0) with scalariform pitting in the metaxylem, (1) with no scalariform pitting (coniferopsid type).
15. Secondary xylem (0) with circular bordered pitting or perforations only, (1) with at least some scalariform pitting or perforations. Scoring of angiosperms based on Metcalfe (1987).
16. Vessels (0) absent, (1) present. Donoghue & Doyle (1989a) treated vessels in the roots only as a third state, but in the present data sets this occurs only in monocots. To preserve the unordered nature of the previous character, monocots could be scored as unknown, but this would obscure the similarity between monocots and other groups in ability to produce the vessel cell type. To preserve this information, we have redefined the character to express this ability and scored monocots as 1.
17. Rays (0) uniseriate or biseriate, (1) at least some multiseriate.
18. Cortical secretory structures (0) absent, (1) cavities, (2) canals.
19. Lignin with (0) no Mäule reaction, (0) Mäule reaction (Gibbs, 1957).
20. (0) Micro- and megasporophylls pinnately organized, (1) microsporophylls pinnately organized, megasporophylls simple, (2) micro- and megasporophylls simple; extant analysis: sporophylls (0) pinnately organized, (2) simple. Chloranthaceae, core Laurales, and Piperaceae

TABLE 1. Nine-angiosperm matrix, extant and fossil taxa. PROG = "progymnosperms" (*Aneurophyton, Archaeopteris*); ELKI = *Elkinsia* of Serbet & Rothwell (1992) = Devonian "seed fern" of Doyle & Donoghue (1992); MEDU = Medullosaceae; CALL = *Callistophyton*; CORD = Cordaitales; CONI = Coniferales; GINK = Ginkgoales; CORY = Corystospermaceae; PELT = *Peltaspermum*; CYCA = Cycadales; GLOS = Glossopteridales; CAYT = *Caytonia*; BENN = Bennettitales; PENT = *Pentoxylon*; EPHE = *Ephedra*; WELW = *Welwitschia*; GNET = *Gnetum*; MAGN = "core" Magnoliales (Magnoliaceae, *Degeneria*, Myristicaceae, Annonaceae); AUST = *Austrobaileya*; CHLO = Chloranthaceae; WINT = Winteraceae; EUDI = eudicots (Ranunculidae, *Nelumbo*, Trochodendrales, Hamamelidales); ARIS = Aristolochiaceae; PIPE = Piperales (Piperaceae, Saururaceae); NYMP = Nymphaeales (Nymphaeaceae, Cabombaceae); MONO = monocots. ? = character state unknown; – = character not included; A = 0/1; B = 0/2; C = 1/2; D = 1/3; E = 2/3.

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          1         2         3         4         5         6         7         8
 12345678901234567890123456789012345678901234567890123456789012345678901234567890123456789012
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CORD 1001?0000?11000001?2010?000121110??001010?000?0????00000?000??-00?????A0?00???????
CONI 1001?000001101000202010?100?2010000110101000000001000000000000-00?????A0?00???????1
GINK 1001?000001121000102010??000211000110?10100000000000000000000-00????010000???????1
CORY ??0300000?20100001?00201100021?1??0111110?1????????000???00??-00?????A0000???????
PELT ???3100?0?????????00100100021?1??0110??0?0????????000??????-00????01000????????
CYCA ??02?000001110001200010?1000?11010110?10100000000000000000000-00????010000???????
GLOS 1002?10?0?1??0000??00?000000020100111?11?0???0????000???00??-00?????A000????????
CAYT 1003?1010?????????00200?10020100111110?1????????000??????-00?????10000???????
BENN 1002?0001?11001012?10301011 0?0110?110?2011???0???0000??000??-00????010000???????
PENT 1002?0000?2?201010?10301 0??02010011 0?20?1????????000???00??-00????010000???????
EPHE 1111?0000111210110121 1?01112011002 0?2110100010100000000000-00????010?00???????0
WELW 1111?1101011210112121 1?01112011001 0?21?111111100000000100-00????010000???????
GNET 1112?110111111?11012111?0?1110110 2?0?2??111111100000000?00-00????120?10???????1
MAGN 1022?1111111D01110100201?100?0?001110?2012210011011111110001 1-000100000000100A0000?
AUST 1012?1112111201110100201?100?0?001110?3012210011011111110000 1-?000001111020010000?
CHLO 1012?111211120111010301?1?1?0?001110?301221001 0?1111110?001-?12??0111112011?0000
WINT 1002?1111111301010100201?100?0?0011?0?3012210011011111110000 1-000000111002001110 1
EUDI 1004?111B111301?10100201?10A?0?0013?0?3012210011011111110000 0-010A01111102000 1A000
ARIS 1024?1110111301110100201?100?0?001110?301221001 0?111111??121-?01111111 00?10010000
PIPE 1024?1113111101110100301?101?0?001110?301221A011011111111010 1-102?111201A200B10111
NYMP 1004?111011130?0?0?00201?100?0?001110?E012210011001111111000-?0A??100000200D11011
MONO 10???111?11110?1?0100201?100?0?001110?3012210011011111111020-?0111101?00100??700?
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are scored as unknown to allow equivalence of their uniovulate carpels with the condition in Gnetales; however, Piperales as a taxon in the nine-angiosperm data set are scored 0, because Saururaceae have multiovulate carpels.

21. Ovule position (0) appendicular, (1) terminal.

22. Cupule (0) radial, lobed, (1) absent, (2) anatropous, (3) orthotropous unlobed; extant analysis: (0) absent, (1) anatropous, (2) orthotropous.

23. Outer integument derived from two appendages (0) absent, (1) present.

24. Ovules per anatropous cupule or potential homolog (0) several, (1) one.

25. Microsporangia (0) terminal, marginal, or adaxial, (1) abaxial. Microsporangia vary from abaxial to adaxial in angiosperms, but we have scored them as unknown because of the highly modified nature of angiosperm stamens. It is problematical whether the different positions of the pollen sacs of angiosperms, which are unique in being fused lengthwise to the sporophyll, can be equated with conditions recognized in other seed plants.

26. Microsporangia (0) free, (1) fused at least basally.

27. Microsporophylls (0) spiral or in more than one whorl, (1) in a single whorl. Chloranthaceae are scored as unknown to allow equivalence of the three-lobed androecium of *Chloranthus* with the whorled microsporophylls of Bennettitales and Gnetales.

28. Strobili (0) lacking or simple, (1) compound. Of states in the inflorescence character of Donoghue & Doyle (1989a), spikes and racemes are scored as potentially homologous with compound strobili, solitary flowers with simple strobili; cymes are not represented, except in association with solitary flowers.

29. Seeds (0) absent, (1) radiospermic, (2) platyspermic. Omitted in the extant data set (*Gnetum* is the only unequivocally radiospermic taxon).

30. Integument (0) simple, (1) with sclerotesta and sarcotesta.

31. Megasporangium with (0) lagenostome, (1) simple pollen chamber.

32. Micropyle (0) normal, (1) tubular. Angiosperms were scored as unknown in Doyle & Donoghue (1992), because their ovules are so reduced, but we have rescored

TABLE 2. Morphological matrix, extant taxa. CYCA = Cycadales; GINK = *Ginkgo*; CONI = Coniferales; EPHE = *Ephedra*; WELW = *Welwitschia*; GNET = *Gnetum*; MAGN = "core" Magnoliales (Magnoliaceae, *Degeneria*, Myristicaceae, Annonaceae); WINT = Winteraceae; CHLO = Chloranthaceae; CALY = Calycanthaceae; LAUR = "core" Laurales (*Hortonia*, Monimiaceae, Atherospermataceae, Siparunaceae, *Gomortega*, Hernandiaceae, Lauraceae); SAUR = Saururaceae; PIPE = Piperaceae; ARIS = Aristolochiaceae; NYMP = Nymphaeales (Nymphaeaceae, Cabombaceae); RANU = Ranunculidae; TROC = Trochodendrales; MONO = monocots. ? = character state unknown; - = character not included; A = 0/1; B = 0/2; C = 1/2; D = 1/3; E = 2/3.

```
          1         2         3         4         5         6         7         8
 12345678901234567890123456789012345678901234567890123456789012345678901234567890123456789012
CYCA -?00-0-000--10001201000-1000-1-0-00---00-00000000000000000000000???010000???????
GINK -001-0-000--21000100000-1000-1-0-00---00-00000000000000000000000???010000???????1
CONI -001-0-000--01000200000-100?-0-0-00---00-00100000100000000000000????A0000???????1
EPHE -111-0-001--21011010101-0111-0-1-01---11-10100010100000000000000???010?00???????0
WELW -111-1-010--21011210101-0111-0-1-00---11-11111111000000001000000???010000???????
GNET -110-1-011--11?11010101-0?11-0-1-01---1?-11111111000000000?00000???120?10???????1
MAGN -020-1-111--D0111011010-?100-0-0-10---10-22100110111111100011?000100000000100A0000?
WINT -000-1-111--30101011010-?100-0-0-10---20-22100110111111100001?000000111002001110O1
CHLO -010-1-121--2011101?020-?1?1-0-0-10---20-22100110?1111110?001??12??011111201l?0000
CALY -010-1-111--20111011010-?100-0-0-1?---20-221001?0?11111?00111000000000100?02103000??
LAUR -01B-1-111--2011101?010-?100-0-0-11---10-22100110?11111000111O?0001110?12?12?000?
SAUR -022-1-131--10?1?011020-?101-0-0-10---20-22100110?11111101001010Z?1112010200010111
PIPE -0?2-1-131--1011101?020-?101-0-0-10---?0-22110110111111?10??01?102?1112011?0?210111
ARIS -022-1-101--30111011010-?100-0-0-10---20-22100110?111111??121??011111100?10010000
NYMP -002-1-101--30?0?0?1010-?100-0-0-10---C0-22100110011111111000O?0A??1000002O0D11011
RANU -002-1-101--D0111011010-?100-0-0-12---20-22100110111111102000101O1??11?1?200??1000
TROC -002-1-121--30101011010-?101-0-0-12---20-22100110?11111000000?1?00111110200010?0?
MONO -0??-1-1?1--10?1?011010-?10?-0-0-10---20-22100110?111111102O0?0111101?00100??00?
```

them as normal, since they certainly have nothing closely comparable to the gnetalian–bennettitalian state.

33. Nucellus (0) not vascularized, (1) vascularized.

34. Nucellar cuticle (0) thin, (1) thick; extant analysis: redefined as (inner) integument (0) fused most of the way to the nucellus and (1) free nearly to the base, which seems to have the same distribution but is better documented in extant taxa.

35. Pollen with (0) tetrad scar, (1) sulcus, (2) no aperture, (3) three colpi; extant analysis: (0) sulcus, (1) no aperture, (2) three colpi. Conifers are scored as having a tetrad scar in the nine-angiosperm data set, based on primitive fossil representatives, but as sulcate in the extant data set. The disulculate pollen of Calycanthaceae is scored as unknown to allow derivation from either sulcate or inaperturate; they were scored as state 1 in Donoghue & Doyle (1989a), but this state included sulcate, inaperturate, and sulculate.

36. Pollen symmetry (0) radial, (1) bilateral. As in Doyle & Donoghue (1992), we score *Gnetum* as unknown, because its pollen has global rather than radial or bilateral symmetry. We also score angiosperms with radial pollen as unknown, not only because their symmetry is unlikely to be homologous with radial symmetry in the sporelike pollen of primitive seed plants, but also because it is correlated with other characters included in the matrix: globose shape in Winteraceae, three colpi in eudicots. Uninformative in the extant data set.

37. Pollen (0) nonsaccate or subsaccate, (1) saccate.

38. Saccus structure (0) eusaccate (alveolae detached from nexine), (1) protosaccate (alveolae continuous from tectum to nexine).

39. Exine structure (0) spongy alveolar, (1) honeycomb alveolar, (2) granular, (3) columellar; extant analysis: (0) alveolar, (1) granular, (2) columellar. Unordered for reasons discussed in text. Nymphaeales are scored as uncertain because Osborn et al. (1991) reported that Cabombaceae are columellar.

40. Exine striations (0) absent, (1) present. Doyle & Donoghue (1992) scored *Gnetum* as unknown, on the grounds that its tectum is so reduced that any striations would have been lost; this is now supported by ultrastructural observations that the tectal spines of *Gnetum* resemble striations of *Ephedra* and *Welwitschia* (Gillespie & Nowicke, 1992).

41. Megaspore tetrad (0) tetrahedral, (1) linear.

42. Megaspore wall (0) thick, (1) thin, (2) absent (ordered). Ordering of this character is in keeping with the treatment of thin and absent as one state in Doyle & Donoghue (1986, 1992).

43. Microgametophyte with (0) more than four nuclei, (1) four nuclei, (2) three nuclei. In Doyle & Donoghue (1986, 1992), the three-nucleate state of angiosperms was omitted and angiosperms were scored as unknown (to allow derivation from either state), but this state is a potential synapomorphy of angiosperms in the present data sets.

44. Sperm transfer (0) zooidogamous, (1) siphonogamous. Conifers are scored as zooidogamous in the nine-angiosperm data set, based on lack of a sulcus in primitive fossil representatives (cf. Doyle & Donoghue, 1992), but siphonogamous in the extant data set.

45. Megagametophyte (0) monosporic, (1) tetrasporic.

46. Egg (0) cellular, (1) free-nuclear.

47. Early embryogenesis (0) free-nuclear, (1) cellular.

48. Fertilization (0) single, (1) double. See discussion in text. Calycanthaceae lack double fertilization (Loconte & Stevenson, 1991), but because this is associated with apomixis (Davis, 1966) we score them as unknown.

49. Embryo (0) without feeder, (1) with feeder.

50. Seed germination (0) hypogeal, (1) epigeal. Angiosperm data from de Vogel (1980) and Endress (1983); contrary to Loconte & Stevenson (1991), Endress reports that germination of *Austrobaileya* is epigeal.

51. Companion cells in phloem (0) absent, (1) present.

52. Microsporangia (0) various, (1) in two pairs.

53. Endothecium (0) absent, (1) present.

54. Pollen germination (0) in pollen chamber, (1) on stigma.

55. Megagametophyte (0) large, (1) eight-nucleate. The larger tetrasporic embryo sacs of Piperaceae are conservatively scored as unknown, although they show similarities with the eight-nucleate type.

56. Endosperm (0) absent, (1) present.

57. Radicle (0) persistent, (1) replaced by adventitious roots.

58. Habit (0) woody, (1) herbaceous. Groups with interfascicular cambium not producing normal secondary xylem are scored as unknown.

59. End-wall pits or vessel perforations (0) multiple, (1) simple.

60. Sieve-tube plastids (0) starch, (1) PI type, (2) PII type. See text for addition of PII type, scoring of Magnoliales (Behnke, 1988). Core Laurales were scored as unknown in Donoghue & Doyle (1989a), but the basic state with the ingroup arrangement assumed here is PI.

61. Oil cells (0) absent, (1) present.

62. Benzylisoquinoline alkaloids (0) absent, (1) present. Uninformative in the nine-angiosperm data set.

63. Stipules (0) absent, (1) adnate-axillary. Other stipule types are scored as unknown.

64. Chloranthoid teeth on leaf margins (0) absent, (1) present.

65. Perianth (0) more than two whorls (or spiral or chaotic), (1) two whorls, (2) absent. Donoghue & Doyle (1989a) scored Trochodendrales as having one whorl, but because this state is autapomorphic in the present data set we have rescored the group as unknown.

66. Perianth symmetry (0) various, (1) at least calyx trimerous.

67. Stamen number (0) various, (1) multiples of three.

68. Stamens (0) laminar, (1) with well-differentiated filament.

69. Pollen (0) boat-shaped, (1) globose. Groups with saccate and sporelike pollen scored as unknown because it is unclear whether their shape conditions can be compared with those in nonsaccate, basically monosulcate groups.

70. Pollen size (0) large (> 50 μm), (1) medium, (2) small (< 20 μm) (ordered). Previously this character was used only in the angiosperm study (Donoghue & Doyle, 1989a). We have scored taxa with saccate pollen (except *Caytonia*) as uncertain (0/1), for two reasons. First, saccate pollen tends to be conspicuously larger and more massive than pollen of nonsaccate groups, suggesting that there is a functional correlation between presence or absence of sacs and size. If so, scoring saccate groups on the angiosperm-based size scale of Donoghue & Doyle might excessively weight transitions between saccate and nonsaccate and produce spurious groupings among nonangiospermous taxa. Second, it is possible that the more appropriate comparison is between size of nonsaccate pollen grains and size of the central body (nexine) in saccate pollen, which is often much smaller than total grain size.

71. Tectum (0) continuous or finely perforate, (1) foveolate-reticulate. We have modified the definition of state 1 from semitectate-reticulate in Donoghue & Doyle (1989a) and rescored *Austrobaileya* as having this state, since its relatively large foveolae and rounded muri seem more comparable to the sculpture of Chloranthaceae and other reticulate groups than the much more finely perforate sculpture of groups such as Magnoliales.

72. Aperture membrane (0) (nearly) smooth, (1) sculptured. Conifers are scored as unknown in the nine-angiosperm data set because a sulcus is absent in primitive forms. Scoring of Aristolochiaceae is based on SEM photos of *Saruma* pollen kindly provided by Long Huo (Guangzhou); scoring of Piperales is based on Bornstein (1989) and Doyle & Hotton (1991).

73. Supratectal spinules (0) absent, (1) present. Scoring of Piperales is based on Bornstein (1989) and Doyle & Hotton (1991).

74. Endexine (0) thick, laminated, (1) absent, (2) thin, nonlaminated, except under apertures. Unordered for reasons discussed in the text. Following Chlonova & Surova (1988), we have rescored Chloranthaceae as having endexine, not unknown as in Donoghue & Doyle (1989a).

75. Hypanthium (0) absent, (1) present.

76. Ovules per carpel (0) several, (1) one apical. A third state in Donoghue & Doyle (1989a), one basal, is represented only in Piperaceae, which are therefore scored as unknown.

77. Fruit (0) dehiscent, (1) berry, (2) drupe (with endocarp), (3) dry indehiscent. As noted by Loconte & Stevenson (1991), the spongy, indehiscent or irregularly dehiscent fruits of Nymphaeaceae (Cronquist, 1981), scored as dehiscent in Donoghue & Doyle (1989a), are better characterized as berries. Winteraceae were scored as unknown in Donoghue & Doyle (1989a), for either dehiscent or berries, but because the dehiscent condition is restricted to *Takhtajania*, which appears to be nested within the family (Vink, 1988), we have rescored them as having berries.

78. Testa (0) multiplicative, (1) non-multiplicative.

79. Exotesta (0) normal, (1) palisade.

80. Tegmen (0) normal, (1) sclerotic.

81. Nutritive tissue (0) endosperm only, (1) endosperm plus perisperm. Megagametophyte tissue might be considered a third state, but this would be redundant with endosperm formation (character 56).

82. Chromosome number (0) $n = 6$–8, (1) $n = 12$–16. Donoghue & Doyle (1989a) defined state 1 as $n = 12$–19, but because numbers above $n = 12$ are of uncertain and potentially complex origin, we have redefined the states and scored taxa with $n > 16$ as unknown. A third state in Donoghue & Doyle (1989a), $n = 10$–11, is represented only by Calycanthaceae, which are therefore scored as unknown. Data on non-angiospermous groups from Ehrendorfer (1976).

RIBOSOMAL RNA CHARACTERS. 1–86: Characters from the 18S subunit, in terms of positions in soy.

1: 93; 2: 120; 3: 131; 4: nucleotide not present in soy; 5: 132; 6: 134; 7: 176; 8: 181; 9: 189; 10: 190; 11: nucleotide not present in soy (between 191–192); 12: 200; 13: 220; 14: 222; 15: 236; 16: 239; 17: 240; 18: 241; 19: 242; 20: 244;

TABLE 3. Ribosomal RNA matrix. Order of taxa as in morphological matrix. R = A/G; Y = C/T; M = A/C; K = G/T; S = C/G; W = A/T; H = A/C/T; B = C/G/T; V = A/C/G; D = A/G/T; N = A/C/G/T.

```
        1         2         3         4         5         6         7         8
12345678901234567890123456789012345678901234567890123456789012345678901234567
ACCTCGCTTTTSCGCGTBDTCGWAYTGCTMCASGATAGCYGACACCATATTGCCCRGTTTTTGCCTGTGCGTAATACATTAGCTTAG
ACCCTACTTC?CCGCCTGCTCGTACCGCTGCACGATA??TGATACCGT?TTGCTCGTTCGTCGCCT?????AATAAATTAGCTTA?
GYCYWRCTCTTTCGCCTWCCCGWACCRYTTTASGATAGCCGACACCCTGGTGCCCGTTCCTCGCTT??GCCGAATACRTTAGYTTAG
GCCCTAGTTC?TCGCCTTGTCGAATCGTCACWYKRCWGTCGATTCCCCGTCG?CTCATTCCGGATTGCGTGGTACGGGCCAACTTGG
GCCCTWGTTC?TCATCGTGTTGAGCCGTCACACTGCA?AGGGTTTCCCGGTGTCTCGCAGTTGATT?????TACGCGCCAATTTGG
?CCCTAGTCT?TCGTTTTTTCGAGG?ACTTCAGTGCA?TCGACTTCCCGGTGTCTGACGCTCGACT???????A?GGGTCAATTTGG
AGACYGACTCGTYGCTCGCCTATATCGCTCYWKGACTGCCGATTCCATATCGCYYGTGACCCACTCTC?GGTAGTGCGTTGGCCCAT
AGT?CAACTC?TTACTTGCCTAAACCGCTC?WYKRCWGACAATTCTATATCGYTTGTCACCCACTCTCTKRTAGTGCGTTGGCCCAY
AGT?CGACTC?TTGCT?GCCTATACCGCTTCTCGACT?TCGATTCCATATCGCTTGT?ACCCACTC?????TAGTGCGTTGGCCTA?
?GTCT?CCTC?TTGCTCGCCTATACCGTCTCTTGACTGACGATTCCATATCGCTTGCGACCCACTC??T?GTAGTGCGTTGGCCCAT
AGT?CTACTC?TTGCTCGCCCATAYYGCTCCGTGACTTACGATTCCATATCGCTTGTGAYCCACTS???TGTAGTGCGTTGGCCCA?
AGC?TGCCTC?TTACTTGATT?TAC?GTCT?TCGACATACGGTTCCATATCTCCCGATCCCCACTCTCGTTTAGTGCGTTGGCCCAT
AGT?TRCCTCGTTAYTYKMMYATATCGTTTTKCKACW?ACGATTCCATATCTCCTGYCWCCCACTY?TGTTTAGTGCGTTGGCYYAC
AGC?TGMCTC?YTACTTGYYTATACTGYTTCGCRACT?ACGATTCCATAKCGCTTGTGACCCACTCTCYGATAGTGCGTTGGCCCAT
AGC?TRCCTC?CCRCATGTTTGTACCGYTYCWCAACTGATGAYTCCATATCGCCTGWMCCCCRCTC??GGGAAGTGMGTTGGCTTAK
AGT?AGACTC?TTATTTGCCTATA???????TTGACTGCCGATTCCMTATCGGTTGTACCCCACTCTCTGATAGTGAGTTGACCTAT
AGT?CGACTC?TTGCTTGCCCATACCAC??TATGACT?CCAATTCTATATCGCCTGTAACCTACTCTCTGATAGTGCGTTGGCCCAT
AKCKSGMCTC?YYGCNTGMYBAYAYHGYTCCGCGACTGACGAYWCCATAYCGCTCGYRWCCCGCTCTCKGGTARTRCGTTGGYCCAG

  9         0         1         2         3         4         5         6         7
8901234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901234
TCGCTCTATATTAG?CCCCRATCGCCTATTWACCTCGCGYCTATGYCTGGCRYTCTWYRTWCGYSSGGGTTAGGGTGATGGGAGAGR
??????TATACCAG?CCGCAATCGCCTATTAACCCCGTGTTTATGCCCGGCGCTCTACACCCGTCGCGGTTAGGGTGATAGG?G?AG
TCGTYCCATACYARCCCGCAATCGCCTRTTVACYYCGTGTCTATGCCTGGYGCYCYHCATCCGYTCGGGTTAGKGTGATAGGGGARG
?TCTTCCATGCCAACCCGCGACTGCTTATTAAC?TCGCGCCTATRCTCGCCTGCTAACGCCCGCCTCGGTTAGAGCGTCTGGGGAGA
ATCCAGTGTATTCACCCGCAACCACTTATAAATCACGTGCCTATGCCCACTTGCCTCCGTCAGSTTGGG?TTGAACGTCTGA?AGGG
ATGTAATGTACTCA??TGCGGCCACTTATCAACT?CGTGC??????????????????????GGGGGATTAAAACAGCTGG?AGAA
TCGTAATGCGCCAGTCCTCAGYYCTCGGACGGCGCTACGC??????????????????CGCGCGCCTCGGCCGGTGCGATAAGAGAGG
TCGAATTGCGCCAATTCTTGGTCGTCGGACGGTGCTGCGMACGCA?YCGTCATATACTGCGTATTTCTACCGATGYARTAAGRGAGG
?CTAATTGCGC?A??????GGTCGTCGGACG?CGCTGCA?ACGCA?TCGCCGTATTCTGCGCGCCTCGGCCGGTGTGATAAA?GAGG
TCGAATTGCGCCAG??????????TAGGACGGCGCTGCGC??????????????????????????GGCCGGTGTGATAGG???GG
???RWYTGCGCMVG??CTCGGTCGYCGGACGGCGCTGCGC??????????????????CGCGCGCCTCGGCCGGTGTGATAAGAGAGG
TTGTAATGCGCC?ATCCTCAGTCGTCGGACKTCGCTGCGC??????????????????????????????????????AGGGAGG
TTGTATTACGCCAATCCTCAGCTGTCGGWCGGMGCTGCGCTCGCA?CCGCCGCATTCCGCGCGCMTCSGCCGRTGCRATAAGGGAGG
TTGAATTACGCMAA??TTCGGTCGTCGGACGGCGCTGCGC?????CCGCCGTATT?CGCGCGTYYCGGCCGGTGTRATAAGGGAGG
TCGTAGTGCGTCAR?TYTCGGTTGTCGGACGRCSYYAYAYWCGCATTCGCCGYATTYCRCGCAYTYVTSCCGATGCRATAAGGGAGG
TCGATTTACGCCAATCTTCGGTCGTCGGACGGCGCTGCGCACGCA?TCATTGCATTCCGTGTGCTTCGGCCGGTGTGATAAGGGAGG
TCGAAATGC?CAAGGCTTTGGGTGTCGAACGACGCTGCGC??????????????????GCGCGTT?CGGCCGGTGTGATAAGGGAGG
TYGHWGTGCRCCWAYCCTCGGYCGYCGGACGGCGCYGCGCHCGSG?CCGCYGYATTYYGCGCGTYKCGGCCGGTGYGATARGRRARG
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21: 245; 22: 247; 23: 251; 24: 257; 25: 263; 26: 275; 27: 276; 28: 280; 29: 281; 30: 282;
31: 287; 32: 339; 33: 347; 34: 353; 35: 368; 36: 489; 37: 496; 38: 542; 39: 936; 40: 1042;
41: 1050; 42: 1055; 43: 1063; 44: 1065; 45: 1075; 46: 1076; 47: 1085; 48: 1086; 49: 1096; 50: 1100;
51: 1241; 52: 1245; 53: 1300; 54: 1355; 55: 1357; 56: 1358; 57: 1363; 58: 1364; 59: 1365; 60: 1366;
61: 1370; 62: 1371; 63: 1372; 64: 1376; 65: 1404; 66: 1411; 67: 1503; 68: 1514; 69: 1526; 70: 1527;
71: 1528; 72: 1534; 73: 1555; 74: 1564; 75: 1566; 76: 1568; 77: 1573; 78: 1606; 79: 1613; 80: 1666;
81: 1668; 82: 1677; 83: 1724; 84: 1729; 85: 1735; 86: 1747.

87–167: Characters from the 26S subunit, in terms of positions in rice.

87: 740; 88: 741; 89: 748; 90: 750;
91: 759; 92: 769; 93: 784; 94: 790; 95: 791; 96: 797; 97: 830; 98: 834; 99: 865; 100: 866;
101: 904; 102: 1602; 103: 1612; 104: 1620; 105: 1621; 106: 1624; 107: 1637; 108: 1639; 109: 1650; 110: 1651;
111: 1656; 112: 1662; 113: 1663; 114: 1683; 115: 1705; 116: 1708; 117: 1712; 118: 1716; 119: 1723; 120: 1731;
121: 1757; 122: 1758; 123: 1760; 124: 1764; 125: 1777; 126: 1783; 127: 1796; 128: 1949; 129: 1950; 130: 1951;
131: 1958; 132: 1960; 133: 1961; 134: 1962; 135: 1969; 136: 1971; 137: 1973; 138: 1980; 139: 1982; 140: 1983;
141: 1986; 142: 1991; 143: 2000; 144: 2001; 145: 2028; 146: 2031; 147: 2032; 148: 2037; 149: 2040; 150: 2041;

151: 2056; 152: 2057; 153: 2058; 154: 2059; 155: 2060; 156: 2061; 157: 2066; 158: 2072; 159: 2073; 160: 2077;

161: 2078; 162: 2085; 163: 2086; 164: 2088; 165: 2089; 166: 2098; 167: 2102.

168–174: Insertion-deletion events, where gap = A.

168: indel 1 between 131–132 in soy; 169: indel 2 at soy 454; 170: indel 8 between 1526–1527 in soy;

171: indel 9 between 1593–1594 in soy; 172: indel 10 between 768–769 in rice; 173: indel 11 between 1746–1750 in rice; 174: indel 12 between 1756–1758 in rice.

ADDENDUM

VOUCHERS OF SPECIMENS USED IN rRNA ANALYSES

Aristolochia sp. (probably *A. gigantea* Mart. & Zucc.): Iowa State Univ. greenhouse, provided by J. Wendell, Z-94-1, US.

Arundinaria gigantea (Walter) Muehlenb.: Baton Rouge Parish, coll. L. Sims, Z-12-86, LSU.

Asimina triloba (L.) Dunal: Burden Plantation, Baton Rouge, coll. M. Bowen & C. Knaak, Z-16-89, LSU.

Barclaya longifolia Wallich: Suwanee Labs, Lake City, FL, provided by D. Bryne, Z-8-89, LSU.

Brasenia schreberi J. F. Gmel.: Golden Ranch Farm, Gheenes, LA, provided by B. Crain, Z-9-89, LSU.

Calycanthus occidentalis Hook. & Arn.: Hilltop Arboretum, Baton Rouge, coll. C. Knaak, Z-7-89, LSU.

Chloranthus spicatus (Thunb.) Makino: Davis Botany greenhouse B81-804, Doyle 94-2-09-3, DAV.

Colocasia esculenta (L.) Schott var. *antiquorum* (Schott) Hubb. & Roeder: LSU campus, coll. L. Sims, Z-1-85, LSU.

Cycas revoluta (Thunb.): LSU campus, Z-2-85, LSU.

Echinodorus corditollus Griseb.: coll. F. Givens, Z-2-88, LSU.

Encephalartos ferox Bertol. f.: Univ. Illinois greenhouse, provided by D. Nickrent, Z-94-2, US.

Ephedra distachya L.: Davis Arboretum A65-888, Doyle 94-2-09-2, DAV.

Ephedra tweediana C. A. Mey.: Davis Arboretum A67-620, Doyle 94-2-09-3, DAV.

Euryale ferox Salisb.: D. Les s.n., CONN.

Ginkgo biloba L.: LSU campus, coll. L. Sims, Z-3-85, LSU.

Gnetum montanum Markgr.: Davis Botany greenhouse B70-116, Doyle 94-2-09-1, DAV.

Hedycarya sp.: Mt. Kogi, New Caledonia, *L. Thien 600*, NO.

Hosta japonica Tratt.: Baton Rouge, coll. L. Sims, Z-17-87, LSU.

Juniperus ashei Buchholz: Travis Co., TX, coll. J. Drost, Z-22-87, LSU.

Liriodendron tulipifera L.: Baton Rouge, coll. C. Knaak, Z-5-89, LSU.

Magnolia grandiflora L.: LSU campus, Z-4-85, LSU.

Najas guadaliensis (Spreng.) Magnus: coll. C. Knaak, Z-1-89, LSU.

Nuphar luteum (L.) Sibth. & Sm. subsp. *macrophyllum* (Small) Beal: Jefferson Co., MO, *P. H. Raven 27204*, MO.

Nymphaea odorata Ait.: Tammany Parish, LA, coll. F. Givens, Z-21-87, LSU.

Persea barbonia (L.) Sprengel: Hilltop Arboretum, Baton Rouge, coll. C. Knaak, Z-6-89, LSU.

Piper nigrum L.: Iowa State Univ. greenhouse, provided by J. Wendell, Z-94-3, US.

Potamogeton sp.: *P. Hoch 3439*, MO.

Ranunculus acris L.: coll. L. Sims, Z-3-86, LSU.

Sabal minor (Jacq.) Pers.: Burden Plantation, Baton Rouge, coll. J. Drost, Z-20-87, LSU.

Sagittaria lancifolia L.: Baton Rouge, coll. E. Jupe & E. A. Zimmer, Z-13-86, LSU.

Saruma henryi Oliver: US National Arboretum 49482, coll. J. Kress, Z-94-4, US.

Saururus cernuus L.: San Gabriel Parish, LA, coll. R. Chapman, Z-3-88, LSU.

Trochodendron aralioides Sieb. & Zucc.: Taiwan, *S.-M. Chaw 189*, HAST.

Zamia floridana A. DC.: Univ. Illinois greenhouse, provided by D. Nickrent, Z-94-5, US.

Zamia ottonis Miq.: Univ. Illinois greenhouse, provided by D. Nickrent, Z-94-6, US.

SPECIMENS WITHOUT KNOWN VOUCHERS

Avena sativa L.: seeds provided by S. Roux, Univ. Texas.

Cabomba caroliniana A. Gray: San Marcos River, TX, provided by E. Schneider.

Cryptomeria japonica (L.f.) D. Don: Mellingberg Seeds.

Drimys winteri Forster & Forster f.: Berkeley Botanical Garden 45.307, provided by J. Affolter.

Hordeum vulgare L.: cultivar "Himalaya," seeds provided by M. Saghai-Maroof.

Oryza sativa L.: cultivar Lamont, Louisiana Rice Research Station.

Peperomia sp.: Univ. Illinois greenhouse, provided by D. Nickrent.

Pinus taeda L.: seeds provided by O. Stubbs, Louisiana Dept. Wildlife & Forestry.

Pistia stratoides L.: provided by P. Hoch, Missouri Botanical Garden.

Saccharum officinarum L.: line Cavengerie, provided by K. Damann, LSU.

Sorghum bicolor (L.) Moench: cultivar Tx 428R, seeds provided by M. Thomas-Compton, Univ. Nebraska.

Tasmannia lanceolata (Poir.) A. C. Sm.: Berkeley Botanical Garden 60.0052, provided by J. Affolter.

Tripsacum dactyloides (L.) L.: line Tp 112 of J. Beckett, provided by K. Newton, Univ. Missouri.

Triticum aestivum L.: line HW3022, Rohm and Haas seeds, provided by S. G. Bartlett, LSU.

Welwitschia mirabilis Hook. f.: Huntington Botanical Gardens, J. Folsom 13, provided by E. Meyerowitz.

Zea mays L.: cultivar B73, Pioneer HiBred Seeds.

PHYLOGENETIC RELATIONSHIPS OF THE "GREEN ALGAE" AND "BRYOPHYTES"[1]

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Abstract

Considerable progress has been made recently, based on classical morphological characters and newly described ultrastructural features, in understanding the phylogenetic relationships of the tracheophytes to the green algae and bryophytes. Recent technological advances in molecular biology, particularly the advent of the polymerase chain reaction (PCR), have allowed nucleotide sequence data relevant to such large-scale phylogenetic questions to accumulate, especially ribosomal RNA gene sequences (both the large and small subunits) from the nucleus and the chloroplast. We present synthetic cladistic analyses of the green plants that combine and compare available morphological and molecular data sets. Although the resulting phylogenies are poorly resolved in some areas at present, certain conclusions are supported: (1) The green plants are composed of two major monophyletic groups, one containing the "charophyte" green algae and the land plants (i.e., "bryophytes" plus tracheophytes), the other containing the bulk of the classically delimited "green algae" (chlorophytes, pleurastrophytes, and ulvophytes). (2) The land plants are a well-supported monophyletic group, but neither the specific outgroup for the land plants nor the precise relationships among basal lineages of land plants are clear. In many analyses (including the combined molecular and morphological analysis) the three major lineages (i.e., liverworts, hornworts, and mosses) appear to be paraphyletic with respect to the tracheophytes, with an indication that the mosses alone may be the sister group of the tracheophytes; however, in other analyses the "bryophytes" are supported as a monophyletic group. (3) The ulvophytes, chlorophytes, and pleurastrophytes are each supported as monophyletic (with the exception of a few taxa that may be misplaced in the current classification), with the topology: [ulvophytes [chlorophytes + pleurastrophytes]]. Combined analyses of molecular and morphological data offer the greatest potential for resolving these relationships.

Reconstruction of the broad-scale phylogenetic relationships of green plants is important to our understanding of major evolutionary events such as the origin of multicellularity, diversification of life-history strategies, and the conquest of land (Graham, 1985; Mishler & Churchill, 1985). In addition, availability of a well-supported framework of "deep" relationships is necessary for purposes of outgroup comparison in studies of tracheophyte phylogeny (Crane, 1990; Gensel, 1992).

Considerable morphological and ultrastructural data have accumulated over the last two decades that bear on the question of phylogenetic relationships of the green algae and bryophytes to the tracheophytes (e.g., Stewart & Mattox, 1975; Hébant, 1977; Pickett-Heaps, 1979; Crandall-Stotler, 1980, 1981; Brown & Lemmon, 1988; Carothers & Rushing, 1988; Duckett & Renzaglia, 1988; Ligrone & Gambardella, 1988). More recently, comparative molecular data have become

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available as well (e.g., Kantz et al., 1990; Zechman et al., 1990; Lewis et al., 1992; Mishler et al., 1992; Waters et al., 1992; Wilcox et al., 1992). A few attempts have been made to synthesize cladistically this growing database (Mishler & Churchill, 1984, 1985; Sluiman, 1985; Theriot, 1988; Graham et al., 1991; Garbary et al., 1993); none of these, however, have incorporated the newly available molecular data.

Cladistic studies to date suggest that neither the "green algae" nor the "bryophytes" are monophyletic. The green plants appear to be composed of two major lineages and a residuum of unicellular micromonadophytes. One of these major lineages contains the bulk of the classical green algae (Chlorophyceae, Pleurastrophyceae, and Ulvophyceae sensu Mattox & Stewart, 1984). There is an indication that the ulvophytes are basal to the chlorophytes plus pleurastrophytes based on morphological and ultrastructural data (Stewart & Mattox, 1975; Mattox & Stewart, 1984; O'Kelly & Floyd, 1984; Sluiman, 1985). Mishler & Churchill (1985) questioned the monophyly of the ulvophytes because of a lack of morphological synapomorphies to unite that group. This result was supported by a recent molecular study (Zechman et al., 1990) that also found non-monophyly of the chlorophytes. The pleurastrophytes have been treated in three ways: (1) as a separate sister class to the Chlorophyceae (Mattox & Stewart, 1984); (2) as part of the Chlorophyceae (Melkonian, 1990); or (3) as part of the Ulvophyceae (Sluiman, 1989).

The other major lineage of green plants includes the charophycean green algae plus the land plants (i.e., bryophytes plus tracheophytes). The genus *Coleochaete* (or even some part of it alone) appears to be the closest extant sister group of land plants (Graham et al., 1991). The bryophytes are composed of three distinctive lineages (i.e., liverworts, hornworts, mosses) that may be paraphyletic with respect to the tracheophytes. For example, early analyses of morphological data (Mishler & Churchill, 1984), as well as two recent molecular analyses (Mishler et al., 1992; Waters et al., 1992), concluded that the liverworts alone appear to be the basal lineage within extant land plants, i.e., the sister group to the hornworts, mosses, and tracheophytes. General morphological data (Mishler & Churchill, 1984), ultrastructural data (Theriot, 1988), and one molecular data set (Mishler et al., 1992) support a topology with the mosses alone as the sister group of tracheophytes. The phylogenetic placement of the hornworts is not clearly resolved by any of the published data sets. On the other hand, monophyly of the bryophytes (including *Selaginella*) was suggested by a recent cladistic analysis based on sperm ultrastructural data (Garbary et al., 1993).

Molecular sequence data have shown considerable promise for phylogenetic analysis, but they provide no panacea (despite overly optimistic claims in recent literature, e.g., Graur, 1993). In fact, theoretical considerations predict that DNA sequence characters (given their quasi-clocklike evolution and limited number of character states) could be especially problematical in "deep" phylogenetic reconstructions, where considerable asymmetry in branch lengths exists (Felsenstein, 1978; Mishler et al., 1988; Albert et al., 1992; Donoghue & Sanderson, 1992; Albert et al., 1993; Mishler, 1994). Careful evaluation of all potential characters is required; it is necessary to apply to molecular data basic principles of character analysis (for deriving strong, independent hypotheses of character homology) and cladistic analysis (for evaluating the phylogenetic "signal," if any, present in the resulting data set). Theoretical issues that must be faced in large-scale, synthetic analyses include further development of methods for: (1) combining/comparing data sets of fundamentally different natures (including issues of character and character-state weighting; Miyamoto, 1985; Kluge, 1989; Albert & Mishler, 1992; Albert et al., 1992; Donoghue & Sanderson, 1992; Albert et al., 1993); (2) assessing support for clades (e.g., bootstrap vs. the decay index; Mishler et al., 1991; Källersjö et al., 1992); and (3) representing diverse, yet clearly monophyletic, clades (e.g., the exemplar method vs. "compartmentalization"—a new approach involving substituting an inferred "archetype" or hypothetical ancestor for a clade accepted as monophyletic a priori in an inclusive analysis: Mishler, 1994).

When examined carefully, it is evident that different genes are phylogenetically useful at different hierarchical levels. Nuclear-encoded ribosomal RNA gene sequences (both the 26S and 18S subunits) provide data of apparent utility at the highest level of green plant phylogeny (Zimmer et al., 1989; Kantz et al., 1990; Zechman et al., 1990; Lewis et al., 1992; Waters et al., 1992; Wilcox et al., 1992). On the other hand, the 5S rRNA nuclear-encoded gene appears to be too small, and has had too many substitutions (in the positions that vary), to be of use at this level (Bremer et al., 1987; Mishler et al., 1988; Steele et al., 1991). Among chloroplast genes, it appears that the 16S rRNA gene is the most conservative, followed by the 23S rRNA gene (Palmer et al., 1988). Combined data from these two genes have provided corroboration

of some previous morphologically based hypotheses about the relative branching order of the major lineages of land plants (Mishler et al., 1992). In contrast, the protein-coding gene *rbc*L has proven too divergent to be useful *among* these lineages (Manhart, pers. comm.; Mishler, unpublished data), but it has provided consistent systematic characters *within* major lineages. For example, within the mosses the relatively basal position of *Sphagnum* and *Andreaea* is supported, as is the monophyly of the peristomate mosses (with the nematodontous taxa in a more basal position within) and monophyly of the haplolepidious mosses (Mishler, unpublished data).

It is likely that a robust and highly resolved phylogeny can be produced for the green plants in the next few years by integrating classical morphological characters with newly described ultrastructural features and various sets of molecular sequence data from the nuclear and chloroplast genomes. Careful choice of characters and application of proper methods of analysis will be essential, however. The co-authors do not agree unanimously on the homology of all characters as used here, but have found cladistic analysis to be an excellent way to frame arguments objectively. This paper attempts to synthesize data published to date, as a guide (and a target) for ongoing projects in our own and other laboratories. More data are certainly needed, but a comparison of currently available data is of interest in its own right and can assist in the identification of characters and taxa that are crucial for future research. The data sets presented here will be made generally available (annotated MacCLADE files will be sent on request) and, thus, will provide a basis for future synthetic studies.

Materials and Methods

Data sets

Six data sets were assembled in pairs (focused on different phylogenetic levels): two morphological data sets, one large and one small molecular data set, and two combined data sets. The sources and characteristics of these data sets are listed below:

(1) A large-scale green plant morphological data set (GP-MORPH) is focused primarily on the "deep" relationships of the green plants as a whole (thus using many characters from "green algal" systematics). Choice of OTUs was dictated by availability of molecular data for comparative purposes (see GP-MOLEC below). Several representative land plants were included (14 in all). Choice of characters was based on standard criteria of homology and independence (Mishler, 1994); a list of characters and character states can be found in Table 1. Sources include Stewart & Mattox (1975), Mattox & Stewart (1984), Mishler & Churchill (1984, 1985), and Graham et al. (1991). All 110 characters were treated as unordered. A hypothetical ancestor was coded for rooting purposes, based on generalized states in presumed protistan outgroups. The data matrix is shown in Table 2.

(2) A more focused land plant morphological data set (LP-MORPH) is based on the set of OTUs scored by Garbary et al. (1993) for ultrastructural characters of spermatozoids. A list of characters and character states can be found in Table 3. To a modified and somewhat reduced set of their "sperm" characters (numbers 1–65), we added a set of "general morphological" characters (numbers 66–113), beginning with the Mishler & Churchill (1984, 1985) characters (modified). Of these 113 characters, only two (7 and 50) were treated as ordered. Two charophytes were included as outgroups. The data matrix is shown in Table 4.

(3) A large-scale molecular data set (GP-MOLEC) represents a realignment of published nuclear rDNA sequences from selected taxa across the green plants. Full small subunit (18S) sequences were taken from Rausch et al. (1989), Huss & Sogin (1990), Lewis et al. (1992), Wilcox et al. (1992), and others. Partial 18S and large subunit (26S) sequences were taken from Buchheim et al. (1990), Kantz et al. (1990), Zechman et al. (1990), and Chapman & Buchheim (1991). OTUs and sources of data are shown in Table 5. All intron sequences were excluded. Those taxa that seemed repetitive at this phylogenetic level (i.e., multiple, very similar species from the same genus) were deleted, and the alignment was adjusted by eye to take into account this full set of taxa. The data matrix had 61 OTUs, including *Emiliana* and *Anemonia* as outgroups, and 2179 characters (of these, 1833 are from 18S and 346 are from 26S). Only 37 of the OTUs had 26S data available; the remainder were coded with all question marks for this region. A number of OTUs have considerable missing data between primer regions; such positions were coded with a question mark. To be conservative, gaps were also coded as missing data. For the 18S data, 17 regions (totaling 206 positions) were excluded from analysis because they could not be aligned unequivocally. The data set is too large to publish, but an aligned and annotated PAUP file is available from the authors on request.

(4) A smaller "land plant only" molecular data set (LP-MOLEC) was excerpted from the larger set above (GP-MOLEC); the 16 OTUs (including

TABLE 1. List of characters and character states used for data matrix GP-MORPH. See text for source of these characters and Table 2 for the data matrix.

1. Habitat of free-living vegetative stage: 0, freshwater; 1, brackish or marine; 2, terrestrial.
2. Life history: 0, haplontic; 1, diplontic; 2, isomorphic alternation; 3, heteromorphic alternation.
3. Vegetative cell or thallus attached to substrate: 0, no; 1, yes.
4. Radial symmetry, if multicellular: 0, no; 1, yes.
5. Growth form: 0, unicellular or coccoid; 1, multicellular; 2, coenobic.
6. Vegetative cells contiguous in multicellular organism: 0, no; 1, yes.
7. Multinucleate vegetative cells: 0, no; 1, yes.
8. Coenocytic: 0, no; 1, yes.
9. Distromatic foliar thalli: 0, absent; 1, present.
10. Plasmodesmata: 0, absent; 1, present.
11. Parenchyma: 0, absent; 1, present.
12. Vegetative cells form filaments: 0, no; 1, yes, unbranched; 2, yes, branched; 3, yes, multi-axial.
13. Filaments with acuminate tips: 0, no; 1, yes.
14. Vegetative cells or zoospores spindle-shaped: 0, no; 1, yes.
15. Zoospores: 0, absent; 1, present; 2, present, flattened.
16. Autospores/colonies: 0, no; 1, yes.
17. Vegetative cell with flagella: 0, no; 1, yes.
18. Gamete production: 0, holocarpic; 1, heterocarpic.
19. Multiple sporulation/fission: 0, no; 1, yes.
20. Type of sex: 0, isogamy; 1, anisogamy; 2, oogamy.
21. Chloroplast shape: 0, cup; 1, reticulated; 2, lateral cup; 3, H-shaped; 4, bi-polar; 5, sets of complete rings; 6, incomplete rings; 7, multiple disks; 8, spiral; 9, stellate; 10, plate; 11, axile.
22. Pyrenoids: 0, absent; 1, present.
23. Thylakoid membranes traverse pyrenoid: 0, no; 1, yes.
24. Number of flagella on vegetative cells or zoospores: 0, 2; 1, 4; 2, 1; 3, 4+; 4, 0.
25. Retraction of flagella during division: 0, no; 1, yes.
26. Angle of basal bodies relative to direction of motion: 0, angled; 1, perpendicular; 2, parallel.
27. Flagellar beat: 0, trailing-undulating; 1, breast stroke.
28. Basal bodies distant via migration in development: 0, no; 1, yes.
29. Flagella extend to right on motile cells: 0, no; 1, yes.
30. Flagellar apparatus displaying 180 degree rotational symmetry: 0, no; 1, yes.
31. Absolute orientation: 0, counterclockwise; 1, clockwise; 2, direct opposite.
32. Basal body overlap in motile cells: 0, absent; 1, present.
33. Basal body core connection: 0, absent; 1, present.
34. Mitotic spindle type: 0, metacentric; 1, centric.
35. Mitotic spindle closed: 0, absent; 1, present.
36. Spindle collapsing at telophase: 0, absent; 1, present.
37. Cupping microtubules surround centrioles during mitosis: 0, no; 1, yes.
38. Microtubules forming in plane of cell division: 0, absent; 1, present.
39. Phragmoplast: 0, no; 1, yes.
40. Cell plate in cytokinesis: 0, no; 1, yes.
41. Centrioles between nucleus and plane of cleavage: 0, no; 1, yes.
42. Lactate fermentation: 0, absent; 1, present.
43. Chaetophoralean autolysin lyses sporangium: 0, no; 1, yes.
44. Hydrogenase produced by vegetative cells: 0, no; 1, yes.
45. Secondary carotenoids: 0, no; 1, yes.
46. Siphonoxanthin: 0, absent; 1, present.
47. Gelatin liquifaction: 0, no; 1, yes.
48. Photosystem II light harvesting complex: 0, low molecular weight; 1, high molecular weight.
49. Dormant zygote produced: 0, no; 1, yes.
50. Sporulation: 0, absent; 1, present.
51. Zellteilung [vs. sporulation]: 0, no; 1, yes.
52. Common matrix surrounds cells: 0, no; 1, yes.
53. Papillae on vegetative cells: 0, no; 1, yes.
54. Crystalline cell wall: 0, no; 1, yes.
55. Stigma: 0, no; 1, yes.
56. Number of contractile vacuoles: 0, 2; 1, 2+; 2, 1; 3, absent.
57. Apical insertion of flagella: 0, no; 1, yes.
58. Zoosporangia abscise: 0, no; 1, yes.
59. Zoosporangia operculate: 0, no; 1, yes.
60. Zoosporangial exit plug: 0, no; 1, yes.
61. Keeled flagella: 0, no; 1, yes.
62. Urea amidolyase produced: 0, no; 1, yes.

TABLE 1. Continued.

63. Terminal cap: 0, absent; 1, bilobed; 2, platelike.
64. Prominent proximal sheath: 0, no; 1, yes.
65. Organic scales/covering: 0, no; 1, yes.
66. Transverse septum: 0, absent; 1, present.
67. Proximal septum: 0, absent; 1, present.
68. SMAC or system 1 fiber: 0, absent; 1, present.
69. Diaphasis: 0, absent; 1, present.
70. Distal fiber in motile cell: 0, absent; 1, present.
71. Specialized zoosporangia: 0, absent; 1, present.
72. MLS present: 0, no; 1, yes.
73. Glycollate oxidase: 0, no; 1, yes.
74. Oogonium associated with sterile cells: 0, no; 1, yes.
75. Eggs retained in oogonium: 0, no; 1, yes.
76. Apical cell growth: 0, no; 1, yes.
77. Flavonoids: 0, no; 1, yes.
78. Zygote retained: 0, no; 1, yes.
79. Placental transfer cells: 0, no; 1, yes.
80. True antheridia: 0, no; 1, yes.
81. Archegonia: 0, no; 1, yes.
82. Embryo: 0, no; 1, yes.
83. Cuticle: 0, no; 1 yes.
84. Monoterpenes: 0, no; 1, yes.
85. Lunularic acid: 0, no; 1, yes.
86. Elaters: 0, no; 1, yes.
87. Oil bodies: 0, no; 1, yes.
88. D-Methionine distinguished: 0, no; 1, yes.
89. Stomata: 0, no; 1, yes.
90. Vertical division of zygote: 0, no; 1, yes.
91. Pseudoelaters: 0, no; 1, yes.
92. Xylem: 0, no; 1, yes.
93. Phloem: 0, no; 1, yes.
94. Perine on spores: 0, no; 1, yes.
95. Aerial sporophyte axis: 0, no; 1, yes.
96. Columella in sporangium: 0, no; 1, yes.
97. Multicellular rhizoids: 0, no; 1, yes.
98. Leaves on gametophyte (of moss type): 0, no; 1, yes.
99. Articulated peristome: 0, no; 1, yes.
100. Independent sporophyte: 0, no; 1, yes.
101. Branched sporophyte: 0, no; 1, yes.
102. Ornamented tracheid walls: 0, no; 1, yes.
103. True lignin: 0, no; 1, yes.
104. Megaphylls: 0, no; 1, yes.
105. Trichomes: 0, no; 1, yes.
106. Vascular cambium: 0, no; 1, yes.
107. Eustele: 0, no; 1, yes.
108. Seeds: 0, no; 1, yes.
109. Axillary branching: 0, no; 1, yes.
110. Flowers: 0, no; 1, yes.

two charophyte outgroups) used are marked in Table 5. The alignment was adjusted based on the land plant sequences alone. This was done because the phylogenetic resolution was poor with the larger GP-MOLEC data set in this part of the green plants. An aligned and annotated PAUP file is available from the authors on request.

(5) A combined data set (GP-COMB) was produced by combining GP-MOLEC and GP-MORPH. This data set omitted the outgroups *Emiliana* and *Anemonia* from GP-MOLEC and the hypothetical ancestor from GP-MORPH, but otherwise used the full combined data as described separately above for 59 OTUs. No weighting was done.

(6) A smaller combined data set (LP-COMB) that focused on the land plants was produced by combining morphological data from LP-MORPH with sequence data from GP-MOLEC. These data sets are unfortunately severely nonoverlapping; only nine taxa have data in both sets when "composite" OTUs are constructed pairing presumably related, but not identical, taxa. The composition of the nine

TABLE 2. Data matrix GP-MORPH. See Table 1 for list of characters and states, and Table 5 for list of taxa.

	1 0	2 0	3 0	4 0	5 0	6 0	7 0	8 0	9 0	1 0 0	1 1 0
Glycine max	2310110001	1000000102	70??0?????0	??01000011	0?????0??10	100??30000	0?000??000	0?11111111?	?11?000110	0111100001	1111111111
Oryza sativa	2310110001	1000000102	70??0?????0	??01000011	0?????0??10	100??30000	0?000??000	0?11111111?	?11?000110	0111100001	1111111111
Zamia floridana	2310110001	1000000102	70??0?????0	??01000011	0?????0??10	100?030000	0?00000000	0111111111	111?000110	0111100001	1111111100
Psilotum sp.	2310110001	1000000102	70??0?????0	??01000011	0?????0??10	100??30000	0?000??000	0111111111	111?000110	0111100001	1111000000
Equisetum hymale	2310110001	1000000102	70??0?????0	??01000011	0?????0??10	100?030000	0?00000000	0111111111	111?000110	0111100001	1110000000
Atrichum angustatum	2310110001	1000000102	70??0?0?10	??01000011	0?????0??10	1000?30000	0?00000000	0111110111	111?000110	0111111100	0000000000
Fissidens taxifolius	2310110001	1000000102	70??000?10	?101000011	0?????0??10	1000030000	0?00000000	0111111111	1110000110	0111111110	0000000000
Plagiomnium cuspidatum	2310110001	1000000102	70??000?10	?101000011	0?????0??10	1000030000	0?00000000	0111111111	1110000110	0111111110	0000000000
Notothylas breutellii	2310110001	1000000102	71??000?10	?101000011	0?????0??10	1000030000	0?00000000	0111110111	1110000111	1000010000	0000000000
Phaeoceros laevis	2310110001	1000000102	71??000?10	?101000011	0?????0??10	1000030000	0?00000000	0111110111	1110000111	1000010000	0000000000
Porella pinnata	2310110001	1000000102	70??000?10	?101000011	0?????0??10	1000030000	0?00000000	0111111111	1111111000	0000000000	0000000000
Conocephalum conicum	2310110001	1000000102	70??000?10	?101000011	0?????0??10	1000030000	0?00000000	0111111111	1111111000	0000000000	0000000000
Asterella tenella	2310110001	1000000102	70??000?10	?101000011	0?????0??10	1000030000	0?00000000	0111111111	1111111000	0000000000	0000000000
Riccia austinii	2310110001	1000000102	70??00??10	?101000011	0?????0??10	1000030000	0?00000000	0111111111	1111111000	0000000000	0000000000
Coleochaete nitellarum	0010110001	1100100102	1100000010	0101000011	0?????0??11	10000?0000	0?00100000	0111100110	0000000?00	0000000000	0000000000
Klebsormidium flaccidum	00001?0001	0100100000	1100000010	0101000001	0?????0??11	10000?00?0	0000000000	0?10000000	0000000?00	0000000000	0000000000
Micromonas pusila	1?00000000	0000101?0?	01021?000?	??01100000	??????0???1	0000030000	0?00011000	0?00000000	0000000000	0000000000	0000000000
Mantoniella squamata	1?00000000	0000101?0?	0102100000	0101100000	??????0?1?1	0000130000	0?00111000	0000000000	0000000000	0000000000	0000000000
Nephroselmis pyriformis	1?00000000	0000101?0?	0100101001	?101100000	??????0???1	0000021000	0?00110100	0000000000	0000000000	0000000000	0000000000
Pedinomonas minutissima	1?00000000	0000101?0?	01021?0?01	??01100000	??????0???1	0000120000	0?00000100	0000000000	0000000000	0000000000	0000000000
Tetraselmis carteriiformis	1?00000000	0000101?0?	0101121101	0000111100	0?????0???1	0000101000	0000010000	0000000000	0000000000	0000000000	0000000000
Enteromorpha intestinalis	1210110010	0000100011	6101011001	0101100000	0?????0?001	1010??1000	0011010101	00?0000000	0000000000	0000000000	0000000000
Ulva fasciata	1210110010	0000100011	6101011001	0101100000	0??1?0?001	1010??1000	0011010101	00?0000000	0000000000	0000000000	0000000000
Ulothrix zonata	0310110000	0100100010	6101011001	0101100000	0?0??0?001	1010101000	0?01110101	0000000000	0000000000	0000000000	0000000000

TABLE 2. *Continued.*

	10	20	30	40	50	60	70	80	90	100	110
Cymopolia barbata	1111111100	0300000111	710?0?10?1	??01100000	0????????01	0000?31010	0?000?????	0000000000	0000000000	0000000000	0000000000
Batophora oerstedtii	1111110007	0200100110	71??011071	0101100000	0????????01	0000131010	0?07000111	0000000000	0000000000	0000000000	0000000000
Codium decorticatum	1110111100	0300000111	7104011001	0101100000	0????1?101	0000?31000	0?000????7	0000000000	0000000000	0000000000	0000000000
Cladophoropsis membranosa	1210111000	0200100110	?101011001	??01100000	0?????0?001	1000??1001	0?0?0????7	0000000000	0000000000	0000000000	0000000000
Blastophysa rhizopus	1210111001	0200100110	?101011001	0101100000	0?????1?101	1000?3107?	0?00000?01	?000000000	0000000000	0000000000	0000000000
Trentepohlia sp.	2210110001	0200100110	107?011001	0101100?70	??????0??01	10000?1100	1?0????007	11?0010000	0000000000	0000000000	0000000000
Cephaleuros parasiticus	2210110001	0200100110	107?011001	0101100?70	??????0??01	10000?1100	1?07?0007?	11?0010000	0000000000	0000000000	0000000000
Characium vacuolatum	0010000000	0001100010	?1100?1001	1001110100	??????0??01	0001??1000	0?00010?01	00?0000000	0000000000	0000000000	0000000000
Dunaliella parva	1000000000	0000101000	01101?1?01	100??????00	??????0???1	0000?31000	0?000????1	0000000000	0000000000	0000000000	0000000000
Chlamydomonas reinhardtii	0000000000	0000101010	0110001001	1001110100	1??1?0?011	0001101000	0100010101	0000000000	0000000000	0000000000	0000000000
Volvox carteri	0000200000	0000011112	?1?0???101	1001110?00	??????0???1	0101??1000	0?000????1	00?0000000	0000000000	0000000000	0000000000
Chlorococcopsis min	0000000000	0000100010	?1100?1001	1001110100	??????0??01	0001??1000	0?00010001	00?0000000	0000000000	0000000000	0000000000
Draparnaldia plumosa	0010110001	0210100010	6101011001	1001110101	0?1??0??11	1010101000	0100010101	00?0000000	0000000000	0000000000	0000000000
Uronema belkae	0010110001	0110100010	6101011001	1001110101	0?1??0??11	1010101000	0?00010101	00?0000000	0000000000	0000000000	0000000000
Chlamydomonas moewusii	0000000000	0000101010	01?0001?01	100??????00	??????0??11	0011101000	0?000????1	00?0000000	0000000000	0000000000	0000000000
Stephanosphaera pluvialis	0000200000	0000011010	2110101101	1001110100	??????0??11	0111111000	0?000??101	00?0000000	0000000000	0000000000	0000000000
Carteria radiosa	0000000000	0000101010	0111001001	100??????00	??????0??11	0011101000	0?00010?01	00?0000000	0000000000	0000000000	0000000000
Gonium pectorale	0000200000	0000011010	0110?21101	1001110100	??????0??11	0101101000	0?00010101	00?0000000	0000000000	0000000000	0000000000
Chlorella kessleri	0000000000	0000010?1?	?1??0??????	???????0100	?0?1000??1	000??3?000	????0????0?	0??0000000	0000000000	0000000000	0000000000
Chlorella vulgaris	0000000000	0000010?1?	01??0??????	???????0100	?1?0000??1	000??3?000	?1??0????0?	0?00000000	0000000000	0000000000	0000000000
Prototheca wickerhamii	0000000000	0000010?1?	?1??0??????	???????0100	??????0???1	000??3?000	????0????0?	0??0000000	0000000000	0000000000	0000000000
Chlorella protothecoides	0000000000	0000010?1?	?1??0??????	???????0100	?1?0000??1	000??3?000	????0????0?	0??0000000	0000000000	0000000000	0000000000
Chlorella minutissima	0000000000	0000010?1?	?1??0??????	???????0100	?0?0000??1	000??3?000	????0????0?	0??0000000	0000000000	0000000000	0000000000
Neochloris aquaticus	0000001000	0000100010	?1000?1001	2011110100	??????0??01	0000??1000	0?00010101	00?0000000	0000000000	0000000000	0000000000

TABLE 2. Continued.

	1 0	2 0	3 0	4 0	5 0	6 0	7 0	8 0	9 0	1 0 0	1 1 0
Neochloris vigenis	0000001000	0000100010	?1000??001	2011110100	?????0??01	0000??1000	0?00010?01	00?0000000	0000000000	0000000000	0000000000
Pediastrum duplex	0000210000	0000100010	?1?0011001	2011110100	1????0??11	0000?1000	0?01010101	00?0000000	0000000000	0000000000	0000000000
Scenedesmus obliquus	0000210000	0000010010	?1?40???0?	???1110100	???1101??1	0000???000	01000???0?	0000000000	0000000000	0000000000	0000000000
Characium hindakii	0010001000	0001100010	?1000?1001	20?1110100	?????0??01	0000??1000	0?00010?01	00?0000000	0000000000	0000000000	0000000000
Chlorella fusca	0000000000	0000010?1?	01??0?????	??????0100	?1?1101??1	000??3?000	????0?????	0??0000000	0000000000	0000000000	0000000000
Ankistrodesmus falcatus	0000000000	0001010?1?	?1??0?????	??????0100	?????0???1	000??3?000	????0?????	0??0000000	0000000000	0000000000	0000000000
Pseudotrebouxia gigantea	0000000000	0000200?0?	?1000?1001	0?00111100	0?????0???1	0000?31000	0?00010001	00?0000000	0000000000	0000000000	0000000000
Pleurastrum terrestre	0000110000	0100200?0?	?1000?1001	0?00111100	0?????0???1	0000?31000	0?00010001	00?0000000	0000000000	0000000000	0000000000
Characium perforatum	0010000000	0001100010	?1100?1001	010?11?000	?????0??01	0000??1000	0?00010?01	00?0000000	0000000000	0000000000	0000000000
Parietochloris pseudo	0000000000	0000100010	?1100?1001	010?11?000	?????0??01	0000??1000	0?20010001	00?0000000	0000000000	0000000000	0000000000
Friedmannia israelensis	$^{0}/_{2}$000000000	0000200???	?100011001	0100111100	0?????0???1	0000?31000	0?00010001	0000000000	0000000000	0000000000	0000000000
Hypothetical ancestor	1000000000	0000101010	?000000000	?100000000	0?????0?001	0000030000	0000000000	0100000000	0000000000	0000000000	0000000000

OTUs (including *Coleochaete* as outgroup) in this data set is shown in Table 6.

ANALYSES

A number of parsimony analyses were carried out to examine the phylogenetic implications of these data sets alone and in combination. Data sets were compiled and phylogenetic trees examined using MacCLADE, version 3.01 (Maddison & Maddison, 1992). All analyses were carried out using PAUP, version 3.1 (Swofford, 1991) on an Apple Macintosh Quadra 700 with 20 megabytes of RAM. With the larger data sets, heuristic search algorithms were necessary, thus finding of all the maximum-parsimony (MP) trees cannot be guaranteed.

The analyses are presented in eight groups below, using standard numbers that are used for reference in the Results and the Discussion. The PAUP commands (Swofford, 1991) employed in each search are shown. "Decay analysis" performed in some cases refers to the saving of trees longer than the MP tree(s) by the specified number of steps (Bremer, 1988; Graham et al., 1991; Mishler et al., 1991; Donoghue et al., 1992; Källersjö et al., 1992)—the "decay index" is the number of steps parsimony must be relaxed to cause a particular clade to lose its support. For example, a decay index of 2 for a clade means that it is *present* in the semi-strict consensus (Bremer, 1990) of the MP trees plus those that are one step longer (called decay class "1"), but *absent* in the semi-strict consensus of the MP trees plus those that are one or two steps longer (called decay class "2").

Analysis 1. Land plant morphological data alone (LP-MORPH):

1a. All characters; 100 repetitions of RANDOM taxon addition, TBR branch swapping with MULPARS and STEEPEST DESCENT option; decay analysis to 3 steps.

1b. Sperm data alone (i.e., characters 1–65); 100 repetitions of RANDOM taxon addition, TBR branch swapping with MULPARS and STEEPEST DESCENT option; decay analysis to 3 steps. CONSTRAINT analyses were also done (using the same PAUP options), to find the shortest topologies consistent with [mosses + tracheophytes] and [hornworts + mosses + tracheophytes] as monophyletic groups.

1c. General morphological data alone (i.e., characters 66–113); 100 repetitions of RANDOM taxon addition, TBR branch swapping with MULPARS and STEEPEST DESCENT option; decay analysis to 3 steps. CONSTRAINT analyses were also done (using the same PAUP options), to find the shortest topologies consistent with monophyly of the bryophytes.

1d. Sperm data alone from the nine OTUs selected as part of LP-COMB; branch-and-bound search.

1e. General morphological data alone from the nine OTUs selected as part of LP-COMB; branch-and-bound search.

1f. All characters from the nine OTUs selected as part of LP-COMB; branch-and-bound search.

Analysis 2. Green plant morphological data alone (GP-MORPH). CLOSEST taxon addition, TBR branch swapping with MULPARS and STEEPEST DESCENT option.

Analysis 3. Green plant molecular data alone (GP-MOLEC). 18S and 26S data combined:

3a. All OTUs except two outgroups (59 OTUs); CLOSEST taxon addition, NNI branch swapping with MULPARS, followed by TBR branch swapping with MULPARS on the shortest trees found by NNI swapping.

3b. Land plants alone plus two charophyte outgroups (16 OTUs); 10 repetitions of RANDOM taxon addition, TBR branch swapping with MULPARS.

3c. The nine land plant OTUs selected as part of LP-COMB; branch-and-bound search.

3d. Green algae minus charophytes, land plants, *Emiliana*, and *Anemonia* (43 OTUs); CLOSEST taxon addition, NNI branch swapping with MULPARS, followed by TBR branch swapping with MULPARS and STEEPEST DESCENT on the shortest trees found by NNI swapping.

Analysis 4. Green plant molecular data (GP-MOLEC). 18S data alone:

4a. All OTUs including the two outgroups, *Emiliana* and *Anemonia* (61 OTUs); 10 repetitions of RANDOM taxon addition, NNI branch swapping with MULPARS, followed by TBR branch swapping with MULPARS on the shortest trees found by NNI swapping; decay analysis to 2 steps.

4b. Land plants only plus *Coleochaete* as out-

TABLE 3. List of characters and character states used for data matrix LP-MORPH. See text for source of these characters and Table 4 for the data matrix. All characters are considered unordered, except as noted.

1. Apical cell in antheridia: 0, absent; 1, present.
2. Division pattern in young antheridia: 0, four-celled; 1, two-celled.
3. Endogenous antheridia: 0, absent; 1, present.
4. Antheridial stalk: 0, absent; 1, present.
5. Operculum cells: 0, absent; 1, present.
6. Sperm in pollen tube: 0, absent; 1, present.
7. Number of sperm per male structure (ordered character): 0, 1000+; 1, 100–1000; 2, 16–24; 3, 2.
8. Nascent spermatids: 0, paired; 1, not paired.
9. Diagonal spindle in final mitotic division: 0, absent; 1, present.
10. Replication of the centrioles: 0, present; 1, absent.
11. Time of origin of centrioles: 0, always present; 1, sperm mother cells; 2, sperm mother cell progenitor; 3, earlier.
12. Basal bodies (BB) and flagella: 0, two; 1, more than two.
13. Bicentrioles: 0, present; 1, absent.
14. Basal body position: 0, right angles; 1, side-by-side; 2, staggered anterior-posterior; 3, staggered continuous.
15. Proximal extension A: 0, absent; 1, long; 2, short.
16. Proximal extension B: 0, ventral–dorsal; 1, ventral.
17. Stellate transition: 0, present; 1, absent.
18. Connecting fibers between BBs: 0, present; 1, absent; 2, fine filaments with centrin.
19. Basal body structure: 0, monomorphic; 1, dimorphic.
20. BB staggering associated with microtubule growth: 0, absent; 1, present.
21. Regression of lamellar strip: 0, absent; 1, complete; 2, partial.
22. Lamellar strip/anterior mitochondrion elongation: 0, parallel; 1, perpendicular.
23. Spline aperture: 0, absent; 1, present.
24. Spline aperture location: 0, left of center; 1, right of center.
25. Position of developing MLS: 0, adjacent to BBs; 1, beneath BBs.
26. Plaque stratified between blepharoplast: 0, absent; 1, present.
27. Spline/lamellar strip orientation: 0, 90°; 1, 45°.
28. Posterior notch to lamellar strip: 0, absent; 1, present.
29. Lamellar strip position: 0, under all BBs; 1, under anterior BB only; 2, under some BBs.
30. Stray spline microtubule: 0, absent; 1, present; 2, develops late.
31. Accessory band of microtubules: 0, absent; 1, present.
32. Maturational elongation of anterior mitochondrion: 0, absent; 1, posterior.
33. Spline shank: 0, wide; 1, less than 4 tubules.
34. Osmiophilic crest: 0, absent; 1, present.
35. Anterior osmiophilic ridge: 0, absent; 1, present.
36. Changes in BBs at maturity: 0, absent; 1, dense material at tip; 2, BB cartwheel with plug; 3, BB triplets impregnated with matrix.
37. Matrix around BBs: 0, homogenous; 1, mottled.
38. Posterior of the stellate pattern: 0, extracellular or partly; 1, entirely intracellular.
39. Flagellar scales: 0, present; 1, absent.
40. Late blepharoplast with transient core: 0, yes; 1, no.
41. Direction of flagellar emergence: 0, toward side; 1, toward rear; 2, toward anterior.
42. Nuclear shape at maturity: 0, ovoid; 1, elongate.
43. Nuclear posterior shape: 0, not expanded; 1, expanded.
44. Median constriction: 0, absent; 1, present.
45. Spline attached to nucleus: 0, yes; 1, detached at maturity; 2, never attached.
46. Spline growth associated with nuclear shaping: 0, absent; 1, present.
47. Direction of nuclear compaction: 0, outer shell; 1, anterior to posterior; 2, at equal rates along nucleus; 3, general increase in density.
48. Condensed chromatin strands: 0, spaghettilike; 1, perpendicular to spline; 2, spiral-central strand; 3, general compaction; 4, spikes; 5, irregular plates; 6, solid mass from anterior tip.
49. Diverticulum during shaping: 0, absent; 1, present.
50. Number of gyres of nucleus (ordered character): 0, not coiled; 1, 0.5–3; 2, greater than 3.
51. Dense body in anterior mitochondrion: 0, absent; 1, present.
52. Mitochondrion associated with plastids in spermatogenous tissue: 0, absent; 1, present.
53. Mitochondrion associated with plastids in young spermatids: 0, absent; 1, present.
54. Specialized anterior mitochondrion: 0, present; 1, absent.
55. Specialized posterior mitochondrion: 0, present; 1, absent.
56. Additional mitochondrion in anterior of cell: 0, absent; 1, row of mitochondria behind anterior mitochondrion; 2, numerous unspecialized.
57. Origin of anterior mitochondrion: 0, fusion; 1, elongation.
58. Osmophilic material underneath anterior mitochondrion: 0, absent; 1, present.

TABLE 3. Continued.

59. Change from cristae sacs to baffles: 0, absent; 1, present.
60. Monoplastidic sperm: 0, present; 1, absent.
61. Plastid determines division polarity: 0, present—at poles; 1, present—asymmetrical; 2, absent.
62. Starch grains in single plastid: 0, more than one; 1, one.
63. Sperm plastid contacting nucleus: 0, absent; 1, present.
64. Fibrillenscheide: 0, absent; 1, present.
65. Cytoplasmic loss: 0, absent; 1, partial; 2, complete (or tiny remnant).
66. Embryo: 0, absent; 1, present.
67. Cuticle: 0, absent; 1, present.
68. Lunularic acid: 0, absent; 1, present.
69. Elaters: 0, absent; 1, present.
70. Oil bodies: 0, absent; 1, present.
71. D-Methionine: 0, not recognize; 1, recognize.
72. Stomates: 0, absent; 1, present.
73. Vertical division of zygote: 0, absent; 1, present.
74. Xylem: 0, absent; 1, present.
75. Phloem: 0, absent; 1, present.
76. Perine layer on spores: 0, absent; 1, present.
77. Aerial sporophyte axis of moss/tracheophyte type: 0, absent; 1, present.
78. Columella: 0, absent; 1, present.
79. Multicellular rhizoids: 0, absent; 1, present.
80. Leaves on gametophyte (of moss type): 0, absent; 1, present.
81. Independent sporophyte: 0, absent; 1, present.
82. Branched sporophyte with multiple sporangia: 0, absent; 1, present.
83. Tracheids: 0, absent; 1, present.
84. Lignin: 0, absent; 1, present.
85. Long exserted seta of the liverwort type: 0, absent; 1, present.
86. Oil body cells: 0, absent; 1, present.
87. Spore mother cells lobed: 0, absent; 1, present.
88. Capsule 2–4 valved on a regular basis: 0, absent; 1, present.
89. Capsule wall cells with transverse thickenings: 0, absent; 1, present.
90. Thick capsule wall: 0, absent; 1, present.
91. Elongate antheridia: 0, absent; 1, present.
92. Aerial calyptra: 0, absent; 1, present.
93. Paraphyses: 0, absent; 1, present.
94. Costate leaves: 0, absent; 1, present.
95. Peristome: 0, absent; 1, present.
96. Operculum: 0, absent; 1, present.
97. Cylindrical sporogenous layer: 0, absent; 1, present.
98. Transfer cells on gametophyte side: 0, absent; 1, present.
99. Transfer cells on sporophyte side: 0, absent; 1, present.
100. Seed: 0, absent; 1, present.
101. Megaphyll: 0, absent; 1, present.
102. Microphyll: 0, absent; 1, present.
103. Lateral, broad sporangia: 0, absent; 1, present.
104. Exarch maturation of xylem: 0, absent; 1, present.
105. Chloroplast DNA inversion: 0, absent; 1, present.
106. Sporangia borne on leaves: 0, absent; 1, present.
107. Trichomes: 0, absent; 1, present.
108. Flavonoids: 0, absent; 1, present.
109. Retention of zygote: 0, absent; 1, present.
110. Sheathed hairs: 0, absent; 1, present.
111. Polyphenolics induced by sex: 0, absent; 1, present.
112. Parenchyma: 0, absent; 1, present.
113. Beaked mucilage papillae: 0, absent; 1, present.

group (15 OTUs); 10 repetitions of RANDOM taxon addition, TBR branch swapping with MULPARS and STEEPEST DESCENT option.

4c. Land plants only plus *Coleochaete* and *Klebsormidium* as outgroups (16 OTUs); CLOSEST taxon addition, TBR branch swapping with MULPARS and STEEPEST DESCENT option.

4d. Land plants only plus *Coleochaete* and *Klebsormidium*; *Pedinomonas* as outgroup (17 OTUs); CLOSEST taxon addition, TBR branch

TABLE 4. Data matrix LP-MORPH. See Table 3 for list of characters and states. Characters 1–65 are from sperm ultrastructure; 66–113 are from general morphology. The asterisk (*) for character 65, *Lycopodium*, represents a polymorphism between states 1 and 2 (Renzaglia, unpublished); the asterisk for character 86, *Sphaerocarpos*, represents a polymorphism between states 0 and 1 within the order Sphaerocarpales (*Riella* has differentiated cells).

	sperm characters:						general morphology:				
	1	2	3	4	5	6	7	8	9	1	1
	0	0	0	0	0	0	0	0	0	0	0
CHARA	???????00	30?00?020?	??0??0???0	0?00000000?	1100000001	0??1?1?011	20102	00000	0000000000	0000000000	?000000000	0000?00100	000
NITELLA	???????00	30?00?020?	??0?000??0	0?00000000?	1100000001	0001???0?1	20102	00000	0000000000	0000000000	?000000000	0000?00100	000
COLEOC PUL	???????0?0	00?00?0?0?	000?000??0	0000000000?	00?00???00	0000?1??00	00?01	00000	0000000000	0000000000	?000000000	0000?00011	100
COLEOC ORB	???????0?10	00?00?0?0?	000?000??0	0000000000?	00?00???00	0000?1??00	00?01	00000	0000000000	0000000000	?000000100	0000?00011	110
PHAEOCEROS	0011000001	1011111100?	200?101000	0100003001?	1101001101	1110000110	11102	11000	1110000100	0000000000	0000000100	0000?00010	110
NOTOTHYLAS	0011000001	1011111100?	200?101000	0100003001?	1101001101	1110000110	11102	11000	1110000100	0000000000	0000000100	0000?00010	110
MARCHANTIA	0001000001	1012100111	2011101100	0000003001?	1100001011	0010000010	10112	11111	0000000000	0000010000	0000000110	0000000110	110
SPHAEROCARPOS	0001000001	1012100111	2011101100	0010003001?	1100001011	0010000010	10??2	11111	0000000000	00000*0000	0000000110	0000?00110	110
PELLIA	0101000001	1012100111	2011101000	0000003001?	1100101011	0010000010	10112	11111	0000000000	0000101111	0000000000	0000?00110	110
BLASIA	0?01000001	1012100111	2011101100	0000003001?	1100001011	0010000010	10112	11111	0000000000	0000101111	0000000110	0000?00110	110
JUNGERMANNIA	0101000001	1012100111	2011101000	0000003001?	1100101011	0010000010	10112	11111	0000000002	0000101111	0000000010	0000?00110	110
HAPLOMITRIUM	0101000001	10121?0111	2010101000	?00?03001?	1100001571	0010000010	?1??2	11111	0000000000	0000101100	0000000110	0000?00110	110
TREUBIA	0101000001	1012100111	?010101000	?00?03?01?	11?0001???	0??0000??0	?0??2	11111	0000000000	0000101111	0000000??0	0000?00110	110
SPHAGNUM	1101000111	1012101111	1011101012	0100003001?	1100012201	0110000010	01002	11000	1100011111	0000000000	0100010000	0000?00010	110
ANDREAEA	1101100111	101210?111	2011101010	0100003001?	1100012201	0110000010	00002	11000	1001011111	0000000000	1111000010	0000?00010	111
POLYTRICHUM	1101100111	1012100111	2011101011	0110003001?	1100012201	0110000010	00002	11000	1101111111	0000000000	1111111010	0000?00010	110
HYPNUM	1101100111	1012100111	2011101011	0100003001?	1100012211	0110000010	00002	11000	1101111111	0000000000	1111111110	0000000110	110
TAKAKIA	1101100111	1012100111	?011101012	?10?03?01?	1100?????1	0?10000?10	00??2	11000	1001??11?1	0000000000	110?000010	0000?00110	111
LYCOPODIELLA	0?00001?11	10140?020?	010?101000	0?0?001012	10?000??00	0010102000	?0001	11000	1101111000	1111000000	0000000110	0111000110	110
LYCOPODIUM	0?00001011	1012210?0?	010?101000	0100001012	10000?3310	000010?010	0010*	11000	1101111000	1111000000	0000000110	0111000110	110
SELAGINELLA	0??0?01??1	10?2210?0?	200?101000	0100001012	1100007401	0010002010	?0002	11000	1101111000	1111000000	0000000??0	0111000110	110
EQUISETUM	0?00001111	11030?0100	010?111020	1001100011	1110003301	0000111001	2?001	11000	1101111000	1111000000	0000000??0	0?00110110	110
PTERIDIUM	0?00002111	2103210?00	010?111020	1001127011	1110003302	0000111001	2?001	11000	1111111000	1111000000	0000000110	1000111110	110
MARSILEA	0??0?02111	21030?0100	010?111020	0000020011	1100001602	0000101001	2?001	11000	1111111000	1111000000	0000000??0	1000?11110	110
OSMUNDA	0?00002111	2103210?00	010?111020	1001110011	1110003301	0000111001	2?001	11000	1111111000	1111000000	0000000110	1000111110	110
GINKGO	????713?11	?1030?0100	010?1?1020	0001100110	20?02???00	0001127001	2?000	11000	1101?1000	1111000000	0000000??1	1000111110	110
ZAMIA	????713?11	?1030?0100	010?1?1020	0001100110	20?02???00	0001127001	2?000	11000	1101?1000	1111000000	0000000??1	1000111110	110

swapping with MULPARS and STEEPEST DESCENT option.

4e. The nine land plant OTUs selected as part of LP-COMB; branch-and-bound search.

Analysis 5. Green plant molecular data (GP-MOLEC). 26S data alone.

5a. All OTUs that have 26S data; *Pedinomonas* as outgroup (37 OTUs); 10 repetitions of RANDOM taxon addition, TBR branch swapping with MULPARS and STEEPEST DESCENT option.

5b. Land plants that have 26S data; no outgroups (11 OTUs); CLOSEST taxon addition, TBR branch swapping with MULPARS.

5c. The seven land plant OTUs selected as part of LP-COMB that have 26S data; branch-and-bound search.

Analysis 6. Land plant molecular data alone (LP-MOLEC). Each with 10 repetitions of RANDOM taxon addition, TBR branch swapping with MULPARS and STEEPEST DESCENT option:

6a. All data; *Coleochaete* and *Klebsormidium* as outgroups (16 OTUs).

6b. All data; *Coleochaete* only as outgroup (15 OTUs).

6c. All data; *Klebsormidium* only as outgroup (15 OTUs).

6d. All data; no outgroups (14 OTUs).

6e. 18S data only; no outgroups (14 OTUs).

6f. 26S data only; no outgroups (11 OTUs).

Analysis 7. Land plant combined data (LP-COMB). Each a branch-and-bound search:

7a. All data.

7b. General morphological data plus all molecular data.

7c. All morphological data plus 18S molecular data.

7d. All morphological data plus 26S molecular data.

7e. General morphological data plus 18S molecular data; decay analysis to 2 steps.

7f. General morphological data plus 26S molecular data; decay analysis to 5 steps.

Analysis 8. Green plant combined data (GP-COMB). CLOSEST taxon addition, NNI branch swapping with MULPARS, followed by TBR branch swapping with MULPARS on the shortest trees found by NNI swapping; decay analysis to 3 steps.

Results

Analysis 1a. Only one tree island was found, of 9 MP trees at 208 steps (CI = 0.678; RI = 0.877). The strict consensus tree is shown in Figure 1, along with the decay index for each informative branch (obviously, here and in later figures, the terminal branches leading to OTUs cannot decay). Several traditional groups (seed plants, tracheophytes, mosses, hornworts, liverworts, land plants) were well supported by this data set, but note that the resolution among these major lineages was unresolved. Note also that the lycophytes were not supported as monophyletic.

Analysis 1b. Only one tree island was found, of 56 MP trees at 130 steps (CI = 0.708; RI = 0.882). The strict consensus tree is shown in Figure 2, along with the decay index for each informative branch. The decay analysis was completed at 1 step. However, not all trees at 2 and 3 steps less parsimonious could be saved with available RAM, thus decay classes "2," "3," and "4+" in Figure 2 are estimates. Note that relatively few clades were well supported by this data set, but a monophyletic bryophyte clade was moderately well supported. *Selaginella* was placed weakly with the bryophytes. CONSTRAINT analyses showed that MP topologies with a forced Mishler & Churchill (1984, 1985) resolution, i.e., [liverworts [hornworts [mosses + tracheophytes]]], were 133 steps long with this data set.

Analysis 1c. Only one tree island was found, of 8 MP trees at 67 steps (CI = 0.731; RI = 0.919). The strict consensus tree is shown in Figure 3, along with the decay index for each informative branch. The decay analysis was completed at 2 steps. However, not all trees at 3 steps less parsimonious could be saved with available RAM; thus decay classes "3" and "4+" in Figure 3 are estimates. The Mishler and Churchill topology was supported by this data set, but not strongly since trees one step longer have other *paraphyletic* arrangements of the three major bryophyte groups; note, however, that CONSTRAINT analyses showed that MP topologies with forced bryophyte *monophyly* were 70 steps long with this data set. Note that the tracheophytes were strongly supported as monophyletic, as were the lycophytes. Thus it is

TABLE 5. Taxa included in the data sets GP-MOLEC, GP-MORPH, and GP-COMB, with source for rDNA sequence data (GENBANK accession number given, if known). The taxa selected for the data set LP-MOLEC are marked with an asterisk.

Emiliana huxleyi (Lohm.) Hay & Mohler	Bhattacharya et al., 1992
Anemonia sulcata L.	Hendriks et al., 1990 (X53498)
**Glycine max* (L.) Merr.	Eckenrode et al., 1985
**Oryza sativa* L.	Takaiwa et al., 1984
**Zamia floridana* L.	Arnold, unpublished
**Psilotum* sp.	Zimmer et al., 1989
**Equisetum hymale* L.	Hamby, unpublished
**Atrichum angustatum* (Brid.) Bruch & Schimp.	Waters et al., 1992
**Notothylas breutelii* Gott.	Waters et al., 1992
**Phaeoceros laevis* (L.) Prosk.	Waters et al., 1992
**Porella pinnata* L.	Buchheim & Chapman, 1992
**Conocephalum conicum* (L.) Lindb.	Waters et al., 1992
**Asterella tenella* (L.) P. Beauv.	Waters et al., 1992
**Riccia austinii* Steph.	Waters et al., 1992
**Klebsormidium flaccidum* (A. Br.) Silva, Mattox & Blackwell	Waters et al., 1992
**Coleochaete nitellarum* Jost.	Waters et al., 1992
**Fissidens taxifolius* Hedw.	Waters et al., 1992
**Plagiomnium cuspidatum* (Hedw). T. Kop.	Waters et al., 1992
Micromonas pusilla (Butcher) Manton & Parke	Kantz et al., 1990
Mantoniella squamata (Manton & Parke) Desikachary	Kantz et al., 1990
Nephroselmis pyriformis (Butcher) Rayns	Kantz et al., 1990
"Pedinomonas minutissima Skuja"	Kantz et al., 1990
Tetraselmis carteriiformis Butcher	Kantz et al., 1990
Enteromorpha intestinalis (L.) Link	Kantz et al., 1990
Ulva fasciata Delile	Zechman et al., 1990
Ulothrix zonata (Weber & Mohr) Kutz	Zechman et al., 1990
Cymopolia barbata (L.) Lamour.	Zechman et al., 1990
Bathophora oerstedii J. Ag.	Zechman et al., 1990
Codium decorticatum (Woodward) Howe	Zechman et al., 1990
Cladophoropsis membranacea (C. Ag.) Borg.	Zechman et al., 1990
Blastophysa rhizopus Reinke	Zechman et al., 1990
Trentepohlia sp.	Zechman et al., 1990
Cephaleuros parasiticus Karsten	Chapman, unpublished
Characium vacuolatum Lee & Bold	Lewis et al., 1992 (M63001)
Dunaliella parva Lerche	Lewis et al., 1992 (M62998)
Chlamydomonas reinhardtii Dangeard	Gunderson et al., 1987
Volvox carteri f. *nagariensis*	Rausch et al., 1989
Chlorococcopsis minuta (= Ettlia minuta (Arce & Bold) Komarek)	Lewis et al., 1992 (M62996)
Draparnaldia plumosa (Vauch.) Ag.	Buchheim & Chapman, 1992
Uronema belkae Mattox & Bold	Zechman et al., 1990
Chlamydomonas moewusii Gerloff	Buchheim et al., 1990
Stephanosphaera pluvialis Cohn	Buchheim & Chapman, 1991
Carteria radiosa Korschikoff	Buchheim & Chapman, 1992
Gonium pectorale Muller	Buchheim & Chapman, 1991
Chlorella kessleri Fott & Novakova	Huss & Sogin, 1990
Chlorella vulgaris Beij.	Huss & Sogin, 1990
Prototheca wickerhamii Soneda & Tubaki	Huss & Sogin, 1990
Chlorella protothecoides Krug.	Huss & Sogin, 1990
Chlorella minutissima Fott & Novakova	Huss & Sogin, 1990
Neochloris aquatica Starr	Lewis et al., 1992 (M62861)
Neochloris vigenis Archibald	Wilcox et al., 1992 (M74496)
Pediastrum duplex Meyen	Lewis et al., 1992 (M62997)
Scenedesmus obliquus (Turp.) Kutz	Huss & Sogin, 1990
Characium hindakii Lee & Bold	Lewis et al., 1992 (M63000)
Chlorella fusca var. *vacuolata* Shihira & Krauss	Huss & Sogin, 1990

TABLE 5. Continued.

Ankistrodesmus stipitatus (= *A. falcatus* var. *stipitatus* (Chodat) Lemm.)	Huss & Sogin, 1990
Pseudotrebouxia gigantea Hildreth & Ahmadj.	Kantz et al., 1990
Pleurastrum terrestre Fritsch & John	Kantz et al., 1990
Characium perforatum Lee & Bold	Lewis et al., 1992 (M62999)
Parietochloris pseudoalveolaris (Deason & Bold) Watanabe & Floyd	Lewis et al., 1992 (M63002)
Friedmannia israelensis Chantanachat & Bold	Lewis et al., 1992 (M62995)

clear that a major conflict exists between the sperm data (see results of analysis 1b) and the general morphological data.

Analysis 1d. Three MP trees were found, at 65 steps (CI = 0.862; RI = 0.870), the strict consensus of which is shown in Figure 10. Note that as in analysis 1b, bryophyte monophyly was supported.

Analysis 1e. Two MP trees were found, at 35 steps (CI = 0.857; RI = 0.886), the strict consensus of which is shown in Figure 10. Note that, whereas the mosses alone were supported as sister group to the tracheophytes as in analysis 1c, the relative position of liverworts and hornworts was not resolved.

Analysis 1f. Two MP trees were found, at 105 steps (CI = 0.819; RI = 0.832), the strict consensus of which is shown in Figure 10. Note that bryophyte monophyly was supported, unlike the result of analysis 1a.

Analysis 2. 26,300 MP trees were found at 231 steps (CI = 0.550; RI = 0.895), but the search could not be completed because the RAM of the computer was exceeded. Thus, the effectiveness of the heuristic search was diminished and more trees at 231 steps undoubtedly exist than could be saved. A strict consensus of the trees that were saved is shown in Figure 4. Note the poor resolution among green algal and land plant groups.

Analysis 3a. 32 MP trees were found at 2245 steps (CI = 0.458; RI = 0.589). A strict consensus of the trees that were saved is shown in Figure 5. The main groups of land plants were unresolved (in fact, neither the tracheophytes nor the liverworts were supported as monophyletic). *Tetraselmis* appeared as basal to the green algal clade, while the Trentepohliales + Ulvophyceae (minus *Cymopolia* and *Batophora*) formed a monophyletic group basal to the chlorophytes plus pleurastrophytes. *Pleurastrum* was widely separated from the other pleurastrophytes.

Analysis 3b. Only one island of 5 MP trees at 304 steps was found (CI = 0.612; RI = 0.600). In the consensus (not shown), neither the land plants, tracheophytes, nor liverworts were monophyletic.

Analysis 3c. Two MP trees at 127 steps (CI = 0.630; RI = 0.466) were found, the strict consensus of which is shown in Figure 10. The mosses and hornworts formed a monophyletic group, and the liverworts appeared paraphyletic.

Analysis 3d. Only one MP tree, of 1597 steps, was found (CI = 0.501; RI = 0.518; shown in Fig. 6). None of the three classes of green algae sensu Mattox & Stewart (1984: chlorophytes, pleurastrophytes, and ulvophytes) included in this analysis appeared to be strictly monophyletic. The ulvophytes were paraphyletic near the base, and

TABLE 6. Composition of the OTUs used in data set LP-COMB. Morphological data were taken from selected taxa in LP-MORPH (Table 4) and molecular data were taken from selected taxa in GP-MOLEC (Table 5).

OTU	LP-MORPH	GP-MOLEC
COLEOCHAETE	*C. orbicularis*	*C. nitellarum*
PHAEOCEROS	*P. laevis*	*P. laevis*
NOTOTHYLAS	*Notothylas*	*N. breutelei*
MARCHANTIALES	*Marchantia*	*Asterella*
JUNGERMANNIALES	*Jungermannia*	*Porella*
POLYTRICHALES	*Polytrichum*	*Atrichum*
BRYALES	*Hypnum*	*Plagiomnium*
EQUISETUM	*Equisetum*	*Equisetum*
ZAMIA	*Zamia*	*Zamia*

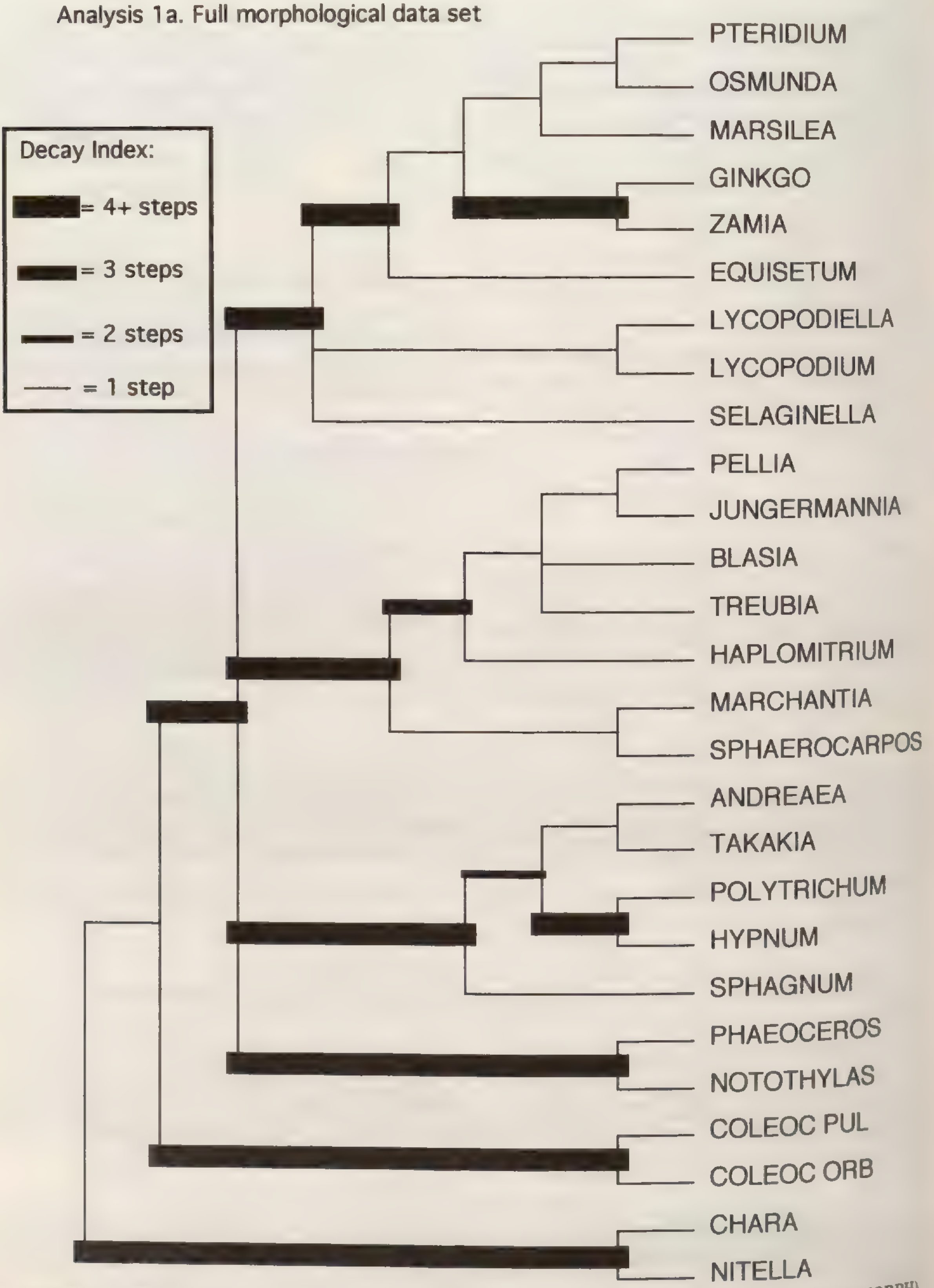

FIGURE 1. Semi-strict consensus of nine most parsimonious trees for the full morphological data set (LP-MORPH). The decay index is shown for each informative branch; thicker branches are better supported.

Analysis 1b. Sperm data only

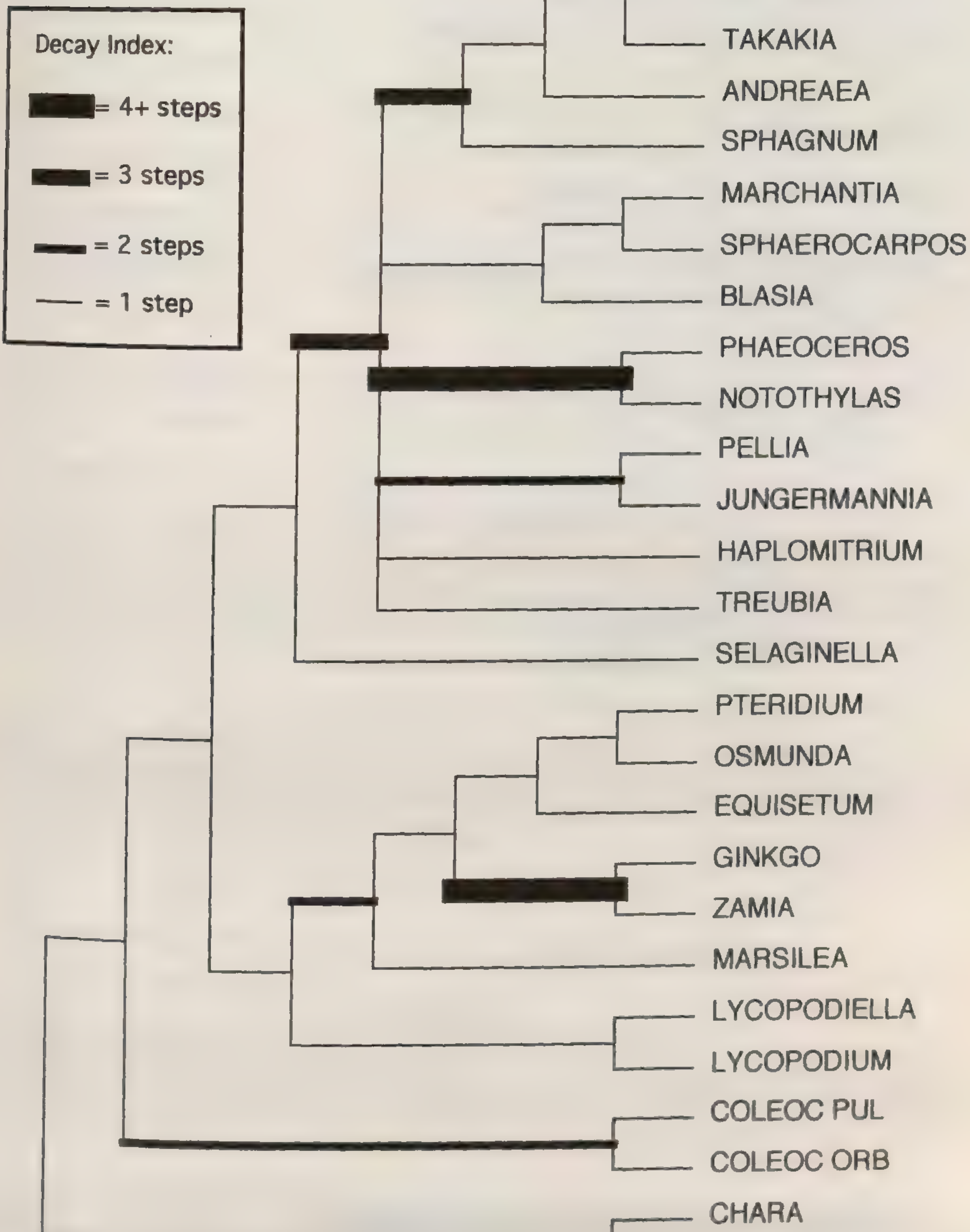

FIGURE 2. Semi-strict consensus of 56 most parsimonious trees for the sperm characters only (characters 1–65, LP-MORPH). The decay index is shown for each informative branch; thicker branches are better supported.

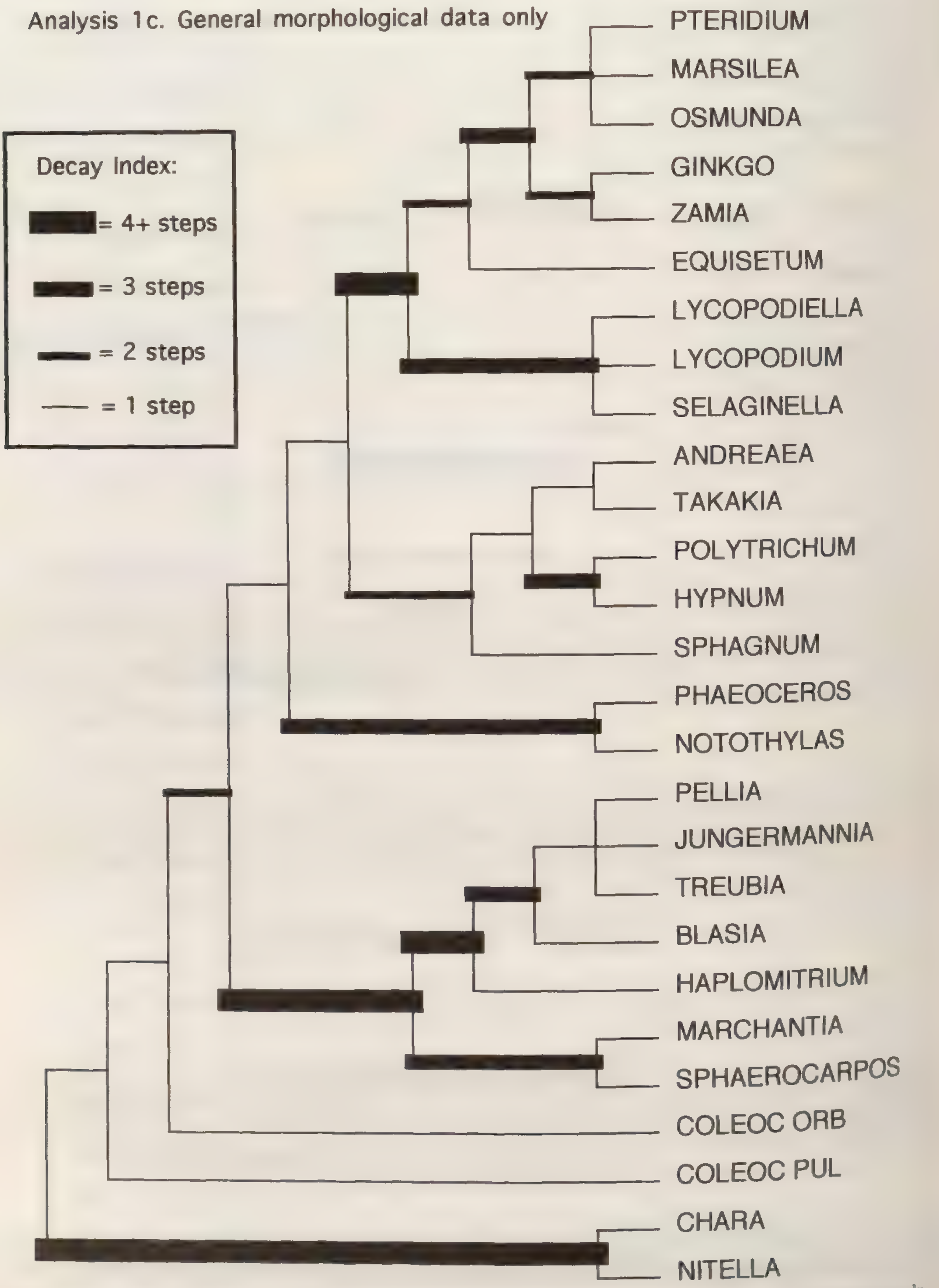

FIGURE 3. Semi-strict consensus of eight most parsimonious trees for the general morphological characters only (characters 66–113, LP-MORPH). The decay index is shown for each informative branch; thicker branches are better supported.

Analysis 2. Morphological data alone

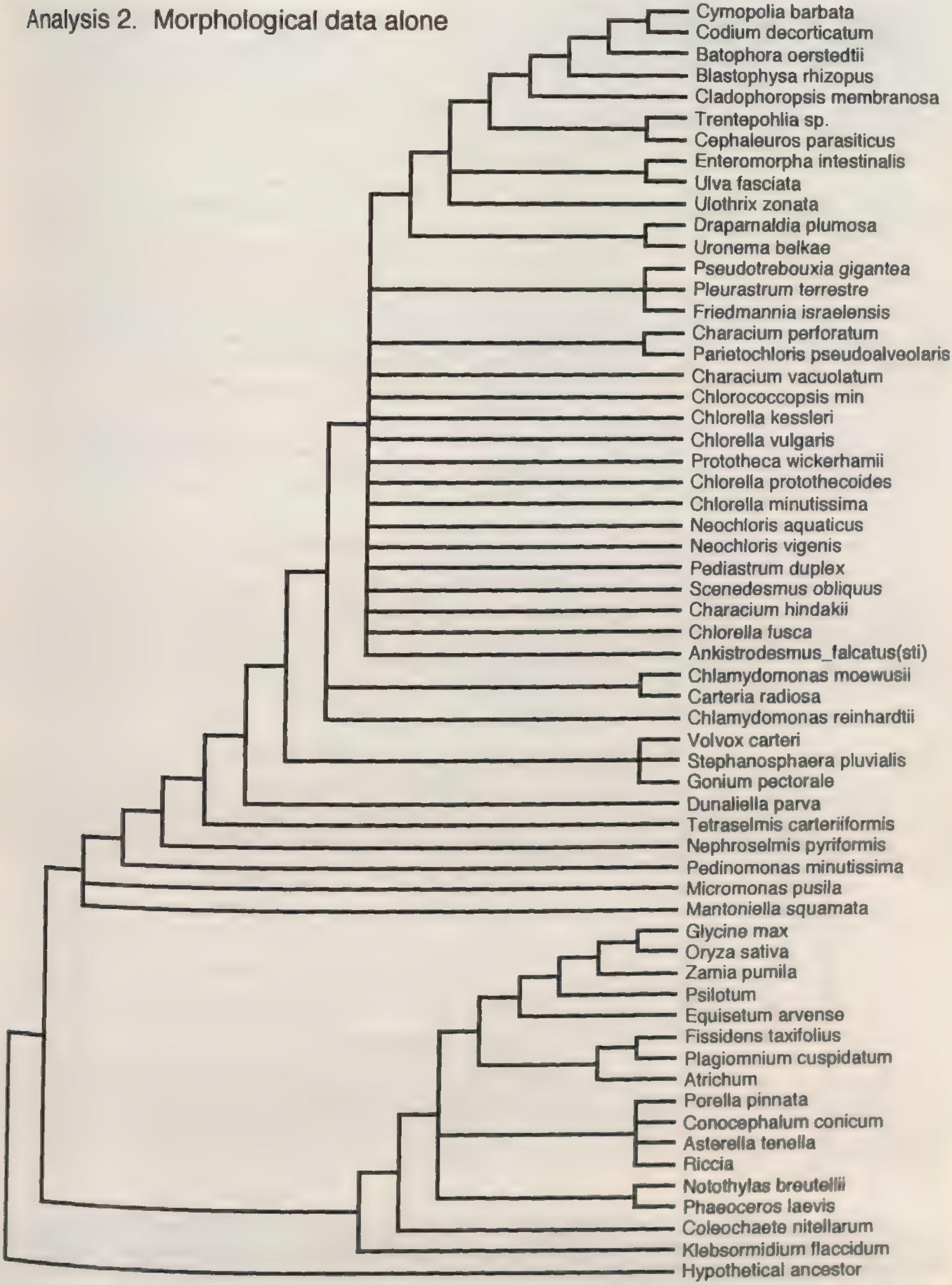

FIGURE 4. Strict consensus of 26,300 most parsimonious trees for the large-scale morphological data set (GP-MORPH). More trees at this length existed that could not be saved.

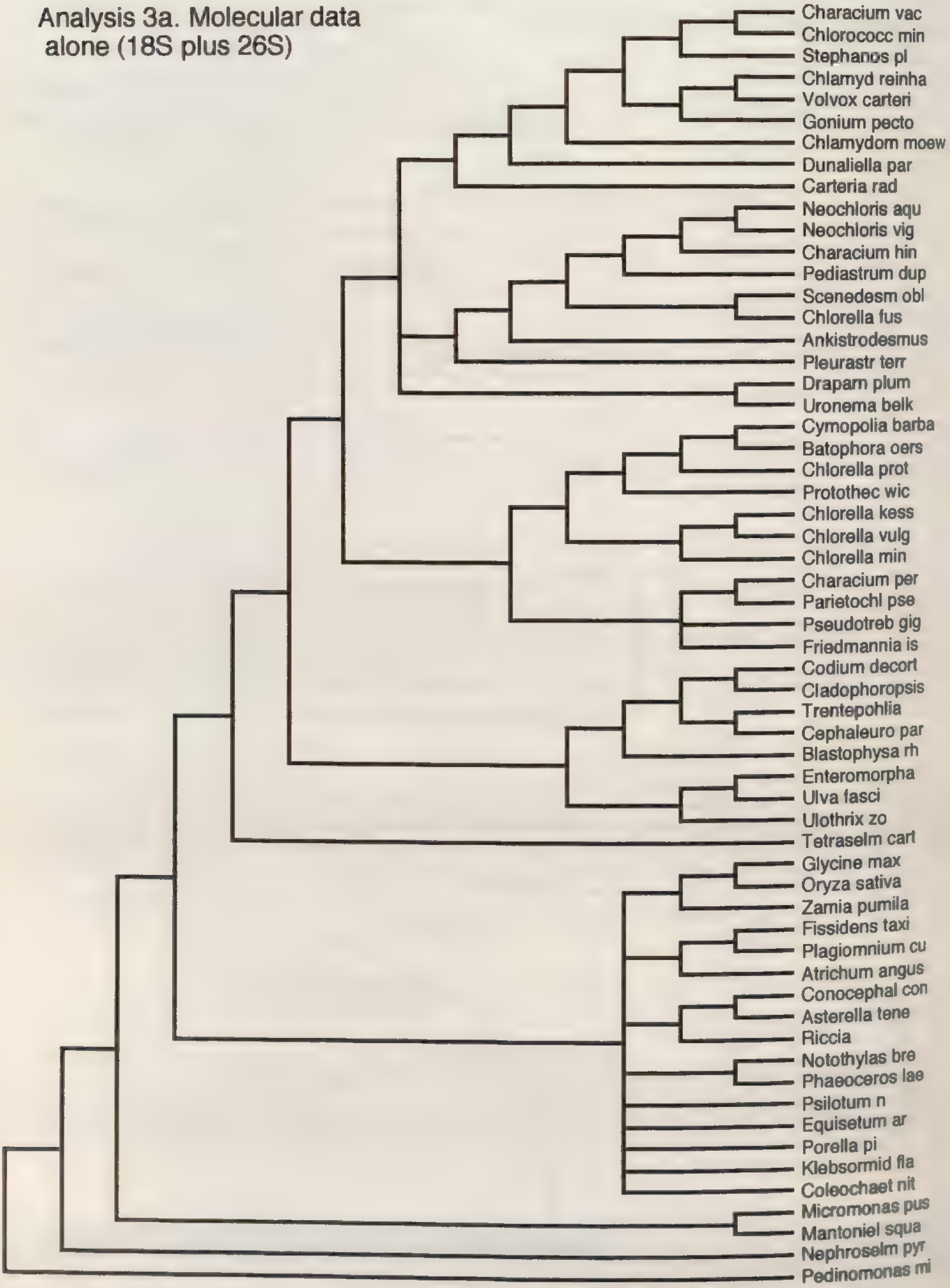

FIGURE 5. Strict consensus of 32 most parsimonious trees for the full molecular data set (GP-MOLEC).

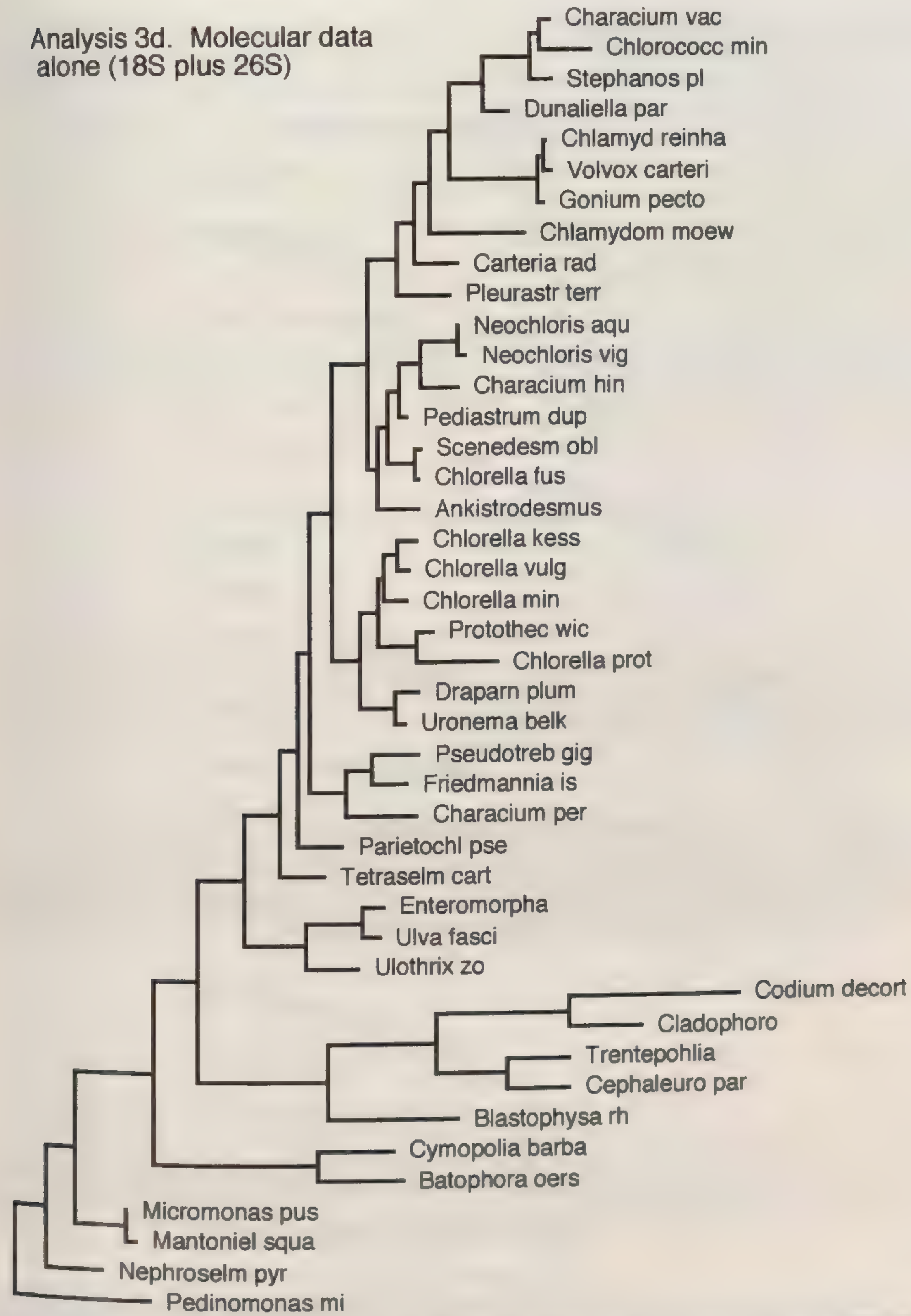

FIGURE 6. Single most parsimonious tree for the green algal taxa with the full molecular data set (GP-MOLEC). The length of each branch is proportional to the number of changes under ACCTRAN optimization.

the pleurastrophytes were paraphyletic above to the chlorophytes + *Pleurastrum*.

Analysis 4a. 84 MP trees at 1888 steps were found (CI = 0.450; RI = 0.589), the strict consensus of which is shown in Figure 7. The land plants were resolved in an unusual topology, with the thallose liverworts alone as the sister group to the tracheophytes and the mosses as the sister group to that clade. The deep branches in the tree,

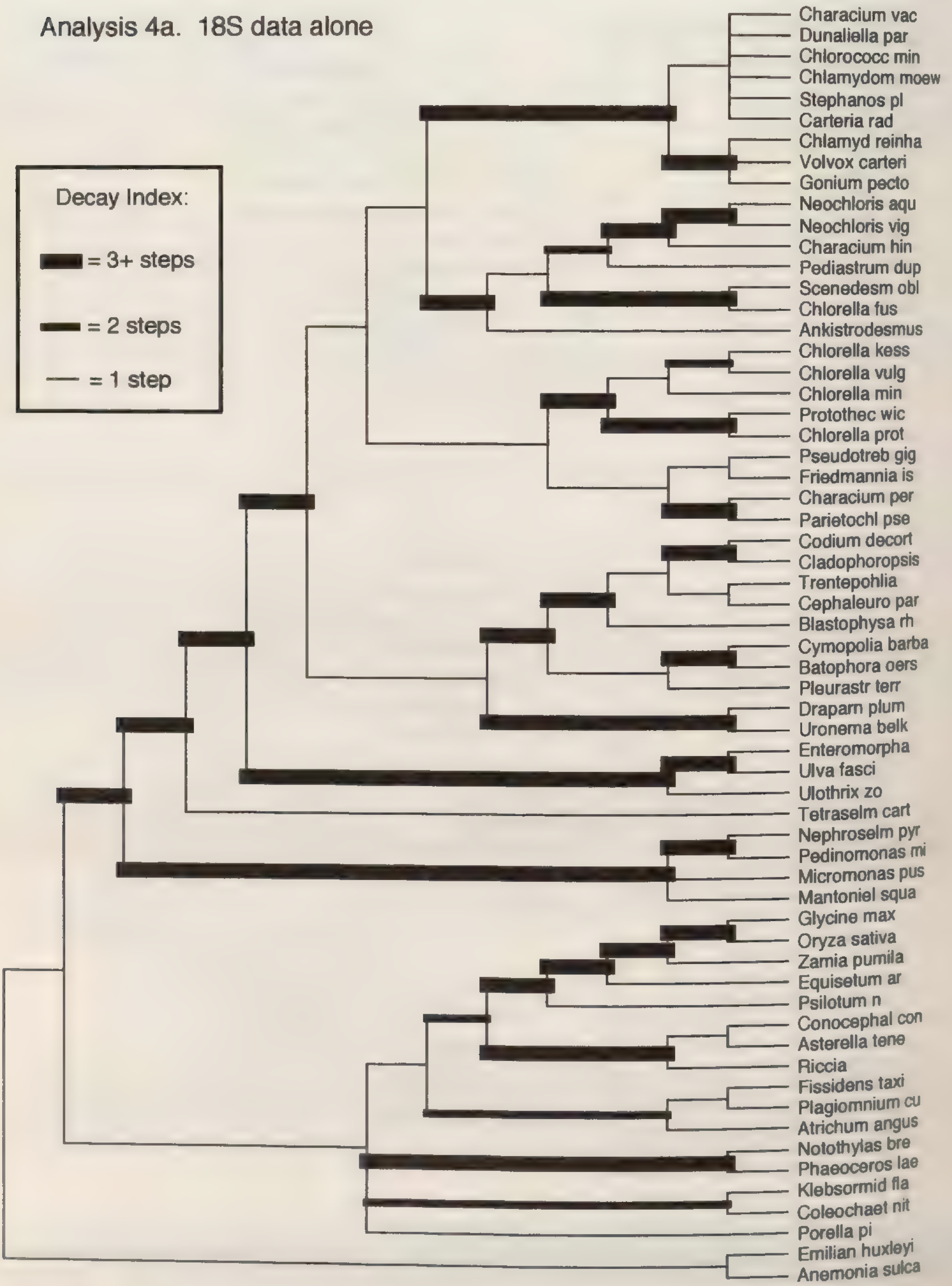

FIGURE 7. Strict consensus of 84 most parsimonious trees for the 18S characters only (GP-MOLEC). The decay index is shown for each informative branch; thicker branches are better supported.

such as the separation of the two major clades of green plants, were relatively well supported. Interestingly, the micromonadophytes were supported as a monophyletic group in this rooting, whereas the ulvophytes were not.

Analysis 4b. Only one MP tree, of 163 steps, was found (CI = 0.632; RI = 0.641; not shown). It had basically the same topology for the land plants as in analysis 4a.

Analysis 4c. Four MP trees, of 176 steps, were found (CI = 0.614; RI = 0.630; not shown). The consensus had basically the same topology for the land plants as in analysis 4a, except less resolved, with the hornworts, *Porella*, mosses, and thallose liverworts plus tracheophytes forming a tetrachotomy.

Analysis 4d. Six MP trees, of 206 steps, were found (CI = 0.607; RI = 0.595; not shown). The consensus had the same topology for the land plants as in analysis 4c.

Analysis 4e. One MP tree was found at 83 steps (CI = 0.627; RI = 0.492; shown in Fig. 10). The bryophytes were supported as a monophyletic group.

Analysis 5a. One tree island was found, of 462 MP trees at 550 steps (CI = 0.493; RI = 0.606). The strict consensus tree is shown in Figure 8; it was very poorly resolved, especially for the land plants; the algal classes were all depicted in different arrangements than in previous analyses.

Analysis 5b. Two MP trees were found at 83 steps (CI = 0.699; RI = 0.699), the strict consensus of which (not shown) had an unusual topology, with neither the tracheophytes nor the mosses potentially monophyletic.

Analysis 5c. Two MP trees at 42 steps were found (CI = 0.667; RI = 0.481), the strict consensus of which (shown in Fig. 10) had the mosses and hornworts together, as sister group to *Equisetum*.

Analysis 6a. One MP tree at 296 steps was found (CI = 0.618; RI = 0.638; shown in Fig. 9). This realignment of molecular data for the land plants alone gave an unusual topology, with the two putative algal outgroups widely separated, and the tracheophytes polyphyletic.

Analysis 6b. Three MP trees at 271 steps were found (CI = 0.642; RI = 0.664), the consensus of which (not shown) had the topology predictable from a re-rooting of Figure 9. The tracheophytes were still polyphyletic, and the mosses plus hornworts were monophyletic.

Analysis 6c. Four MP trees at 250 steps were found (CI = 0.636; RI = 0.669), the consensus of which (not shown) had all major groups unresolved.

Analysis 6d. Three MP trees at 225 steps were found (CI = 0.662; RI = 0.702), the unrooted consensus of which (not shown) had the tracheophytes together, but neither the mosses nor the liverworts were potentially monophyletic.

Analysis 6e. Seven MP trees at 146 steps were found (CI = 0.662; RI = 0.702), the unrooted consensus of which (not shown) had the topology of that in analysis 6d except even less well resolved.

Analysis 6f. Two MP trees at 78 steps were found (CI = 0.692; RI = 0.700), the unrooted consensus of which (not shown) had the same very unusual topology of analysis 5b, with neither the mosses nor the tracheophytes potentially monophyletic.

Analysis 7a. Three MP trees at 240 steps were found (CI = 0.692; RI = 0.632), the strict consensus of which is shown in Figure 10. Note that the major groups of land plants were completely unresolved.

Analysis 7b. Four MP trees at 168 steps were found (CI = 0.655; RI = 0.561), the strict consensus of which is shown in Figure 10. The hornworts, mosses, and tracheophytes were placed together in a trichotomy.

Analysis 7c. Two MP trees at 191 steps were found (CI = 0.723; RI = 0.695), the strict consensus of which is shown in Figure 10. The bryophytes were placed together in a trichotomy.

Analysis 7d. One MP tree at 150 steps was found (CI = 0.760; RI = 0.743), shown in Figure 10. Note that the Mishler & Churchill (1984, 1985) topology, i.e., [liverworts [hornworts [mosses + tracheophytes]]], was present.

Analysis 7e. One MP tree at 124 steps was found (CI = 0.661; RI = 0.600), shown in Figure 11. A similar topology to analysis 4a was present, with [hornworts [liverworts [mosses + tracheophytes]]], but it was relatively weakly supported.

Analysis 7f. One MP tree at 78 steps was found (CI = 0.744; RI = 0.718), shown in Figure 11. Note that the Mishler & Churchill (1984, 1985) topology was again present and was relatively well supported.

Analysis 5a. 26S data alone

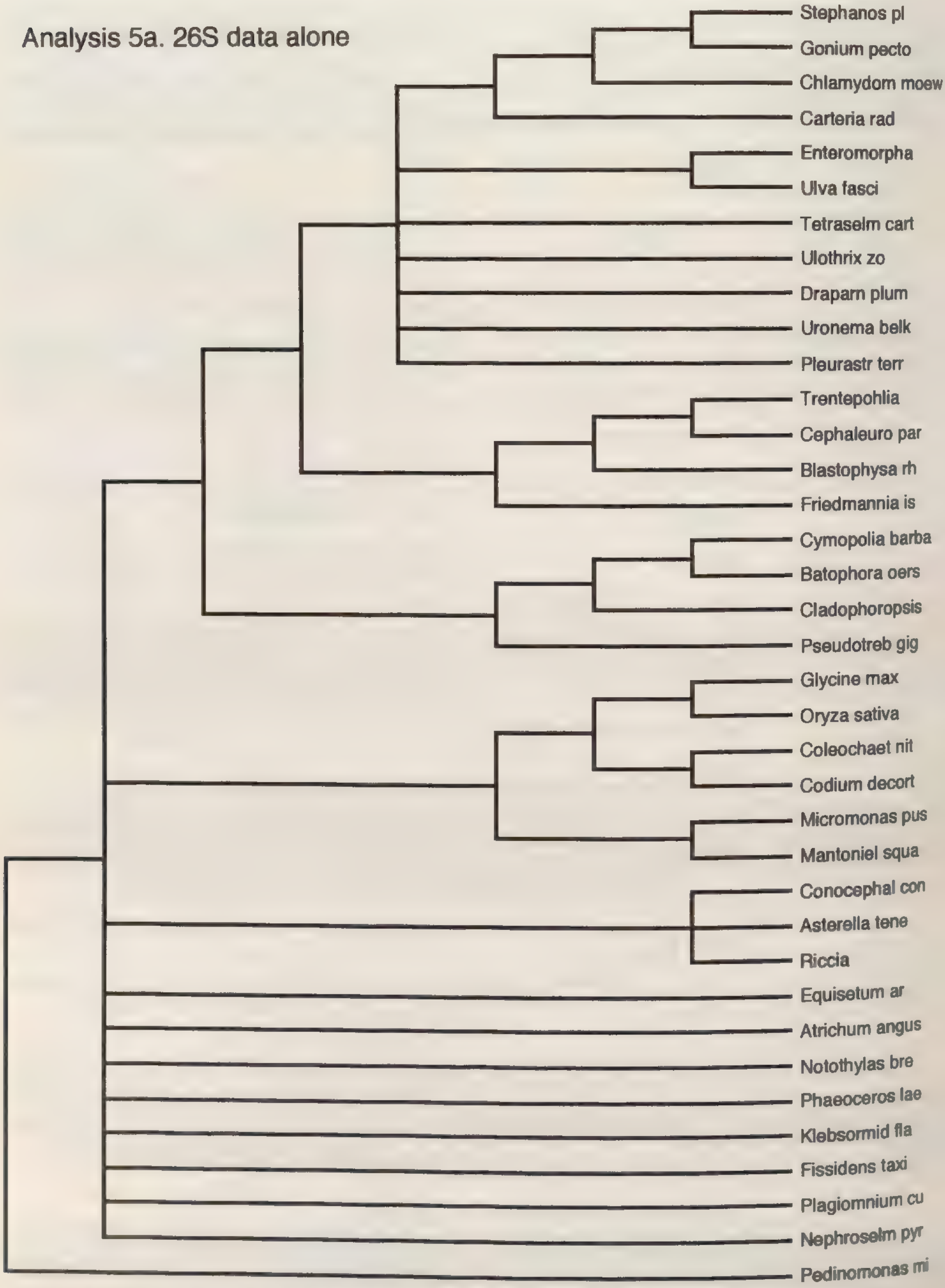

FIGURE 8. Strict consensus of 462 most parsimonious trees for the 26S characters only (GP-MOLEC).

Analysis 6a. Molecular data alone (18S plus 26S); realignment for land plants

FIGURE 9. Single most parsimonious tree for the land plant taxa (plus two charophyte green algae, marked with asterisks) with the full molecular data set (LP-MOLEC).

Analysis 8. Fifteen MP trees at 2511 steps were found (CI = 0.458; RI = 0.654), the strict consensus of which is shown in Figure 12, along with the decay index for each informative branch. The major branches of the tree were relatively well supported and were identical to the Mishler & Churchill (1984, 1985) topology in the "streptophyte" clade (i.e., charophytes + land plants; Bre-

Analyses 1d, 1f, 7c.

Analysis 1e.

Analysis 3c.

Analysis 4e.

Analysis 5c.

Analysis 7a.

Analysis 7b.

Analysis 7d.

mer et al., 1987). Unlike previously published topologies (Zechman et al., 1990), however, the ulvophytes appeared to be monophyletic (with the addition of the problematical genera *Trentopohlia* and *Cephaleuros*), while neither the chlorophytes nor pleurastrophytes (sensu Mattox & Stewart, 1984) were supported as monophyletic groups.

Discussion

In general, it appears that the molecular data were most informative regarding relationships among the green algae. In the combined analysis of molecular data (analysis 3), resolution of the green algal clades was well supported, whereas resolution of land plants was very poor (and where resolution existed, it contradicted ideas of relationships based on other data). The realignment taking into account just the land plants (analysis 6), which might have been expected to yield a better assessment of positional homology (see Mindell, 1991), was of no help in "improving" the results. This difference in resolution could be because of unequal extinction in the two major clades of green plants. As it happens, the extant green algae may more evenly sample the true tree than do the extant streptophytes. Spurious long-branch attraction problems are expected on theoretical grounds to be greater in data types with a restricted number of character states, such as DNA data (Mishler, 1994), and may therefore be seen more frequently in the land plants than in the green algae with the molecular data. A second (not mutually exclusive) reason for the difference in resolution with molecular data might be that most of the green algal OTUs in this analysis were represented by full sequences, whereas most OTUs in the land plant clade were represented by partial sequences.

On the other hand, it appears that the morphological data were most informative about relationships within the streptophyte clade of green plants (sensu Bremer et al., 1987). It is very difficult to code morphological characters broadly across the green plants because of the lack of homologous comparisons among organisms that have evolved such major phenotypic differences. It is also difficult narrowly within the green algal groups because the characters useful at that level are primarily ultrastructural, making sufficient sampling difficult. These difficulties are evidenced by the poor resolution obtained in analysis 2 (Fig. 4). Morphological data coded narrowly for the land plants, however, give a better supported result (e.g., analysis 1). In the latter case, the greater conservatism and larger number of potential character states in complex morphological data may have allowed the recovery of a historical signal obscured in the molecular data.

It has been suggested that even complex morphological character systems may be subject to convergent evolution when under strong selective constraints and, thus, could give misleading phylogenetic reconstructions because of non-independence of characters. It is possible that the conflict observed in analysis 1 between the set of characters derived from the spermatozoid and the general set of characters derived from many parts of the organism (compare Figs. 2 and 3) is due to selective constraints imposed on the streamlined, swimming gamete (cf. Garbary et al., 1993) or on the other morphological features such as conducting tissues. Ultimately, the only means of resolving such conflicts is by investigation of many different characters and character systems. Any one character system (or maybe all) are influenced by constraints that tend to bias phylogeny reconstruction one way or another. The hope is that if one looks at enough character systems the various noise-producing factors will "cancel-out" and a common historical signal can be detected. There is only one known process that can impose a common pattern across all these widely different character systems: phylogeny.

It is difficult to draw any definitive conclusions from the combination of molecular data with morphological data in analysis 7, because the sampling of characters is so uneven that only eight land plants could be included. The combination of both genes together, as well as 18S alone, with the LP-MORPH data set tended to favor a monophyletic bryophyte lineage, whereas the combination with 26S alone tended to favor a paraphyletic arrangement of bryophytes in the same pattern as Figure 3: [liverworts [hornworts [mosses + tracheophytes]]]. The last result is especially intriguing, as neither the morphological data alone (analysis

←

FIGURE 10. Strict consensus trees resulting from maximum parsimony analyses of various character combinations from the reduced data set (LP-COMB) that contains land plants which had both molecular and morphological data available. See text for explanation of which characters were used in each analysis. *Coleochaete* was used for outgroup rooting.

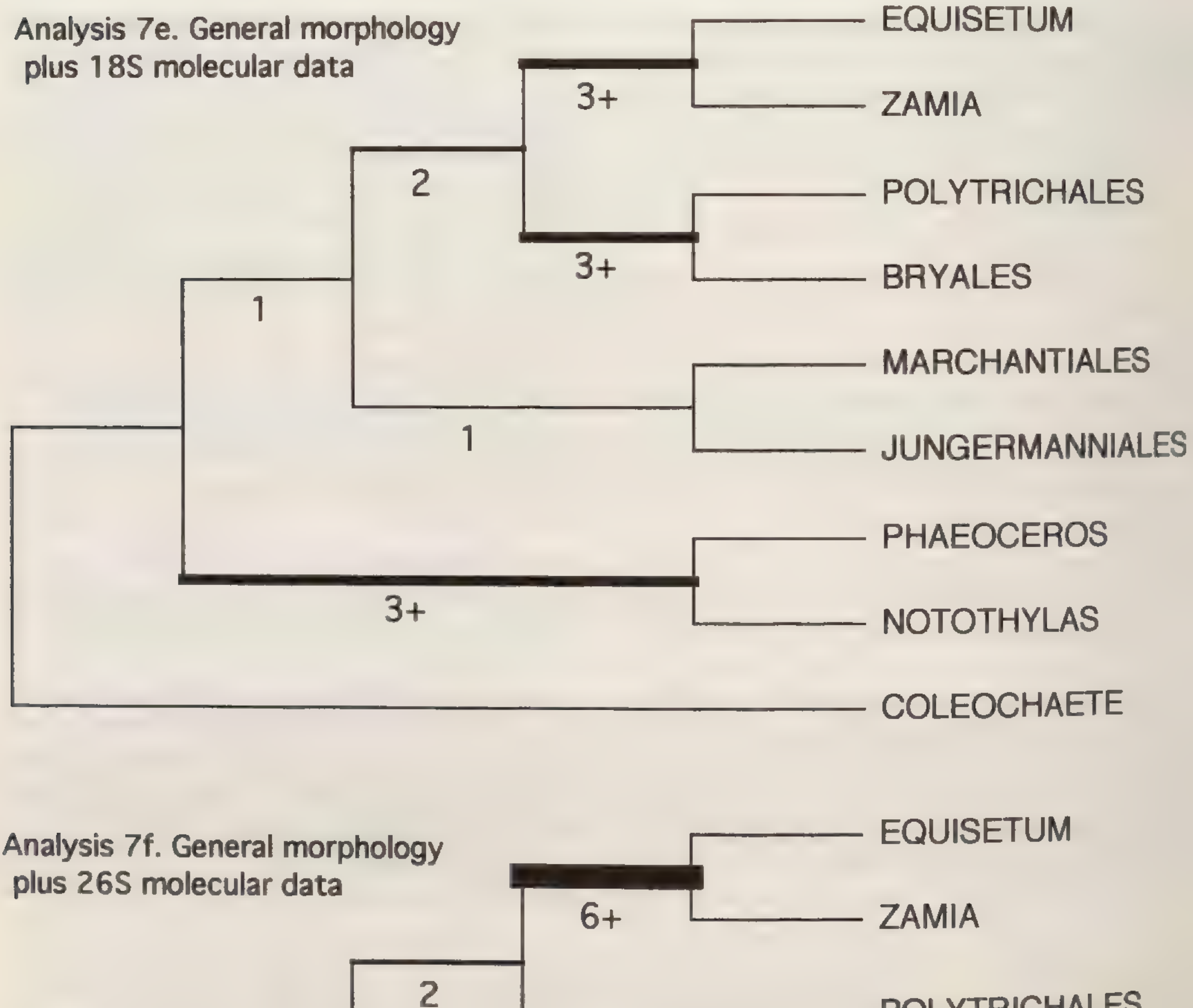

FIGURE 11. Single most parsimonious trees from two different combined analyses of the reduced data set (LP-COMB) that contains land plants which had both molecular and morphological data available. The decay index is shown for each informative branch; thicker branches are better supported.

1f) nor the 26S data alone (analysis 5c) gave such a pattern.

The overall combined analysis of GP-MOLEC and GP-MORPH (analysis 8—Fig. 12) produced a topology that was better resolved than the consensus of the individual analyses of each data set alone. This property is often the case with such "total evidence" analyses (Kluge, 1989). The

Analysis 8. Combined molecular and morphological data

Decay Index:

= 4+ steps

= 3 steps

= 2 steps

= 1 step

Volvox carteri
Gonium pecto
Chlamyd reinha
Characium vac
Chlorococc min
Dunaliella par
Chlamydom moew
Stephanos pl
Carteria rad
Chlorella kess
Chlorella vulg
Prototheс wic
Chlorella prot
Chlorella min
Neochloris aqu
Neochloris vig
Characium hin
Pediastrum dup
Draparn plum
Uronema belk
Scenedesm obl
Chlorella fus
Ankistrodesmus
Pseudotreb gig
Friedmannia is
Characium per
Parietochl pse
Pleurastr terr
Codium decort
Cladophoro
Trentepohlia *
Cephaleuro par *
Blastophysa rh
Cympolia barbe
Batophora oers
Enteromorpha
Ulva fasci
Ulothrix zo
Tetraselm cart *
Glycine max
Oryza sativa
Zamia pumila
Equisetum ar
Psilotum n
Fissidens taxi
Plagiomnium cu
Atrichum angus
Notothylas bre
Phaeoceros lae
Conocephal con
Asterella tene
Riccia
Porella pi
Coleochaet nit
Klebsormid fla
Micromonas pus
Mantoniol squa
Nephroselm pyr
Pedinomonas mi

Chlorophyceae
Pleurastrophyceae
Ulvophyceae
streptophytes
Micromonadophyceae

FIGURE 12. Strict consensus of 15 most parsimonious trees for the large-scale combined data set (GP-COMB). The decay index is shown for each informative branch; thicker branches are better supported. The assignment of green algae to classes according to the concept of Mattox & Stewart (1984) is shown; "streptophyte" indicates charophyte green algae plus embryophytes (sensu Bremer et al., 1987). The unusual placement of three enigmatic taxa is indicated with an asterisk.

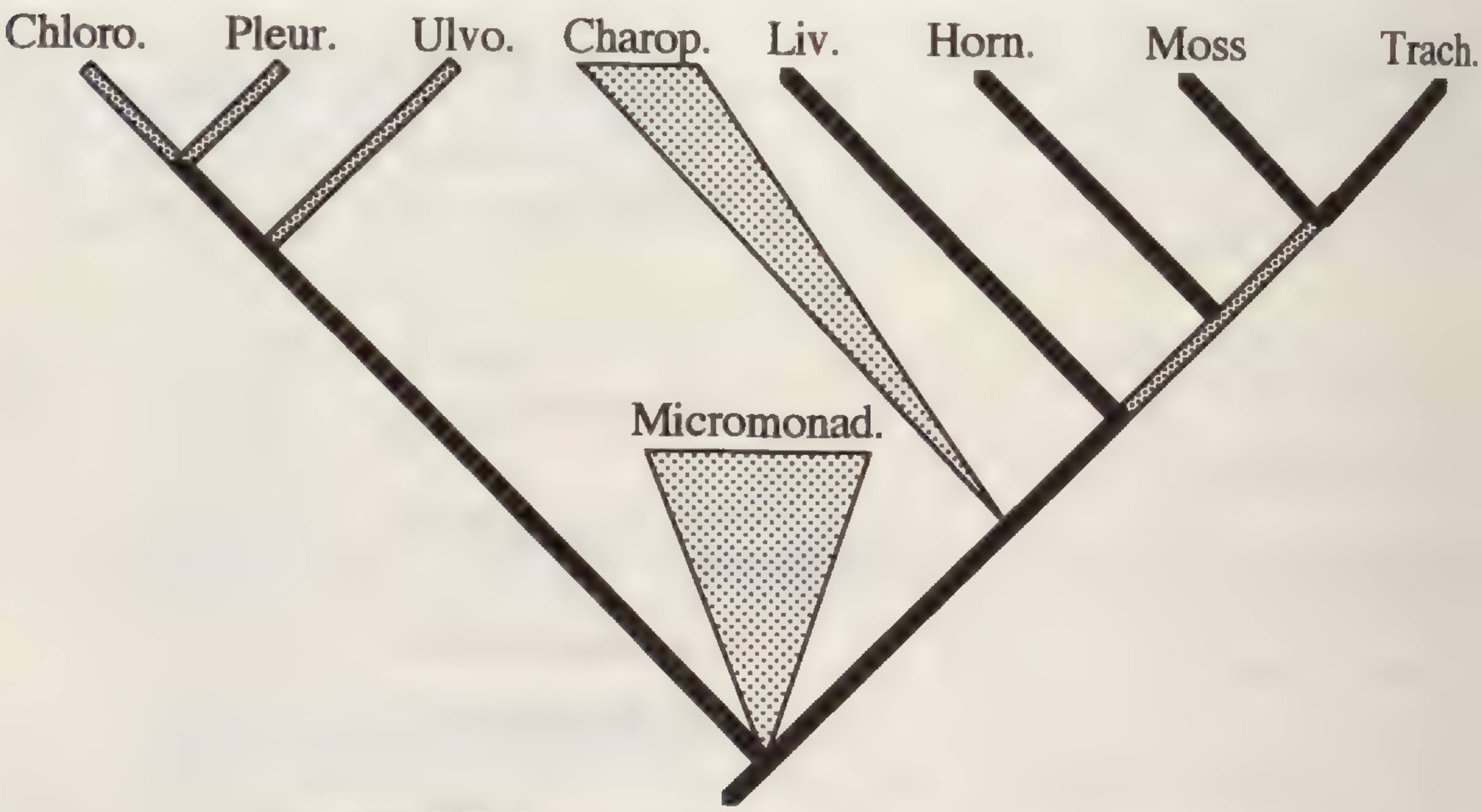

FIGURE 13. A diagram indicating current understanding of cladistic relationships of the five classes of green algae, sensu Mattox and Stewart (1984), and the four major lineages of land plants, sensu Bremer et al., (1987). Branches about which we are confident are shown in black, those for which lesser support exists (and considerable homoplasy) are shown stippled, while two classes of almost certain paraphyly are shown as stippled triangles.

streptophytes were completely resolved, in a topology completely consistent with the early Mishler & Churchill (1984, 1985) analyses and analysis 1a here, despite the fact that neither the morphological data (GP-MORPH in analysis 2) nor the molecular data (GP-MOLEC as a whole in analysis 3 or the separate analyses 4 and 5) alone gave such a topology. The observation of a combined topology that is different from topologies produced in separate analyses of component data sets is not unusual (see discussion of analysis 7 above, and Mishler et al., 1992, for other examples). One potential explanation is that each data set has a common historical signal that is obscured for different reasons in each; the signal might only be observable when the noise in the two data sets cancels out in a combined analysis (Barrett et al., 1991). Carefully coordinated studies are needed to discover the extent to which such an explanation can apply to land plant phylogeny.

The green algal lineages in the overall combined analysis (analysis 8—Fig. 12) had a similar resolution to the consensus of the subanalyses of analysis 3, with the exception that the ulvophytes (plus *Trentopohlia* and *Cephaleuros*) were supported as monophyletic. Several OTUs with long terminal branches (such as *Pleurastrum* and *Ankistrodesmus*) "jump around" in equally parsimonious positions, thus lowering support for the monophyly of both the Pleurastrophyceae and Chlorophyceae as currently circumscribed. Major clades within the chlorophytes, however, such as the taxa with directly opposite basal bodies and those with clockwise absolute orientation of the basal bodies, are supported (as previously found by Lewis et al., 1992).

The results of the various analyses illustrate, if nothing else, how difficult phylogenetic reconstruction is at this deep level, and how no particular data set acts as a "magic bullet." We were working with a mixture of complete, partial, and missing data for a large proportion of the taxa. The two morphological data sets gave conflicting results in some respects, as did the two major molecular data sets. Nevertheless, the combined ("total evidence") analysis (Fig. 12) is reasonably well resolved and well supported, and supports previous phylogenetic and systematic studies to a large extent. It is likely that much of the remaining ambiguity can be removed once more complete data sets are produced. There is still a great deal of work to be done, but we are making progress.

A summation of the currently hypothesized general cladistic relationships of green plants that can be drawn from this and previous studies is shown in Figure 13, along with an indication of places in the phylogeny where uncertainty is greatest. The green plants are composed of two major monophyletic groups, one containing the bulk of the classical "green algae" (chlorophytes, pleurastrophytes, and ulvophytes), the other containing "charophyte" green algae along with the bryo-

phytes plus tracheophytes. A doubtfully monophyletic assemblage of unicellular micromonadophytes is phylogenetically "between" these two major lineages. It appears clear that the ulvophytes are basal to the chlorophytes plus pleurastrophytes, but the exact circumscription of all three classes needs revision. In the other major clade of green plants, the land plants are a well-supported monophyletic group, but neither the specific outgroup for the land plants nor the precise relationships among the charophytes is clear. The bryophytes are supported as a monophyletic group in some analyses; in many analyses, however, including the overall combined analysis (analysis 8—Fig. 12), the three major lineages of bryophytes appear paraphyletic with respect to the tracheophytes, with the topology [liverworts [hornworts [mosses + tracheophytes]]].

The more robust parts of this summary cladogram, though clearly in need of support from future studies sampling more OTUs and more character systems (morphological as well as molecular), can serve as a framework for evolutionary interpretations. It appears reasonably well supported, for example, that multicellularity arose at least twice in the green plants. The diversification of life-history strategies is becoming clearer; from a primitively haplontic life cycle, alternation of generations and diploid-dominant life cycles arose at least twice each. The habitat transition in the movement of plants to land was from fresh water, not from salt water. Within the land plants, several morphological transformations can be reasonably postulated at present, such as the origin of branched, multisporangiate plants from unbranched, unisporangiate ones, and the radiation of conducting cell types (Kendrick & Crane, 1991). The process of inference is difficult, but further refinement of our understanding of phylogenetic relationships will be repaid with a more precise understanding of such evolutionary issues.

Literature Cited

Albert, V. A. & B. D. Mishler. 1992. On the rationale and utility of weighting nucleotide sequence data. Cladistics 8: 73–83.

———, M. W. Chase & B. D. Mishler. 1993. Character-state weighting for cladistic analysis of protein-coding DNA sequences. Ann. Missouri Bot. Gard. 80: 752–766.

———, B. D. Mishler & M. W. Chase. 1992. Character-state weighting for restriction site data in phylogenetic reconstruction, with an example from chloroplast DNA. Pp. 369–403 *in* P. S. Soltis, D. E. Soltis & J. J. Doyle (editors), Molecular Systematics of Plants. Chapman & Hall, New York.

Barrett, M., M. J. Donoghue & E. Sober. 1991. Against consensus. Syst. Zool. 40: 486–493.

Bhattacharya, D., L. Medlin, P. O. Wainright, E. V. Ariztia, C. Bibeau, S. K. Stickel & M. L. Sogin. 1992. Algae containing chlorophylls a + c are paraphyletic: Molecular evolutionary analysis of the Chromophyta. Evolution 46: 1801–1817.

Bremer, K. 1988. The limits of amino acid sequence data in angiosperm phylogenetic reconstruction. Evolution 42: 795–803.

———. 1990. Combinable component consensus. Cladistics 6: 369–372.

———, C. J. Humphries, B. D. Mishler & S. P. Churchill. 1987. On cladistic relationships in green plants. Taxon 36: 339–349.

Brown, R. C. & B. E. Lemmon. 1988. Sporogenesis in bryophytes. Advances Bryol. 3: 159–223.

Buchheim, M. A. & R. L. Chapman. 1992. Phylogeny of *Carteria* (Chlorophyceae) inferred from nuclear and organismal data. J. Phycol. 28: 362–374.

———, M. Turmel, E. A. Zimmer & R. L. Chapman. 1990. Phylogeny of *Chlamydomonas* (Chlorophyta) based on cladistic analysis of nuclear 18S rRNA sequence data. J. Phycol. 26: 689–699.

Carothers, Z. B. & A. E. Rushing. 1988. Comparative morphology of the bryophyte blepharoplast. Advances Bryol. 3: 95–134.

Chapman, R. L. & M. A. Buchheim. 1991. Ribosomal RNA gene sequences: Analysis and significance in the phylogeny and taxonomy of green algae. C. R. C. Crit. Rev. Pl. Sci. 10: 343–368.

Crandall-Stotler, B. 1980. Morphogenetic designs and a theory of bryophyte origins and divergence. BioScience 30: 580–585.

———. 1981. Morphology/anatomy of hepatics and anthocerotes. Advances Bryol. 1: 315–398.

Crane, P. R. 1990. The phylogenetic context of microsporogenesis. Pp. 11–41 *in* S. Blackmore & R. B. Knox (editors), Microspores: Evolution and Ontogeny. Academic Press, London.

Donoghue, M. J. & M. J. Sanderson. 1992. The suitability of molecular and morphological evidence in reconstructing plant phylogeny. Pp. 340–368 *in* P. S. Soltis, D. E. Soltis & J. J. Doyle (editors), Molecular Systematics of Plants. Chapman & Hall, New York.

———, R. G. Olmstead, J. F. Smith & J. D. Palmer. 1992. Phylogenetic relationships of Dipsacales based on *rbc*L sequences. Ann. Missouri Bot. Gard. 79: 333–345.

Duckett, J. G. & K. S. Renzaglia. 1988. Ultrastructure and development of plastids in the bryophytes. Advances Bryol. 3: 33–93.

Eckenrode, V. K., J. Arnold & R. B. Meagher. 1985. Comparison of the nucleotide sequence of soybean 18S rRNA with the sequences of other small-subunit rRNAs. J. Molec. Evol. 21: 259–269.

Felsenstein, J. 1978. Cases in which parsimony and compatibility will be positively misleading. Syst. Zool. 27: 401–410.

Garbary, D. J., K. S. Renzaglia & J. G. Duckett. 1993. The phylogeny of land plants: A cladistic analysis based on male gametogenesis. Pl. Syst. Evol. 188: 237–269.

Gensel, P. G. 1992. Phylogenetic relationships of the zosterophylls and lycopsids: Evidence from morphology, paleoecology, and cladistic methods of inference. Ann. Missouri Bot. Gard. 79: 450–473.

Graham, L. E. 1985. The origin of the life cycle of land plants. Amer. Sci. 73: 178–186.

———, C. F. Delwiche & B. D. Mishler. 1991. Phylogenetic connections between the "green algae" and the "bryophytes." Advances Bryol. 4: 213–244.

Graur, D. 1993. Molecular phylogeny and the higher classification of eutherian mammals. Trends Ecol. Evol. 8: 141–147.

Gunderson, J. H., H. Elwood, A. Ingold, K. Kindle & M. L. Sogin. 1987. Phylogenetic relationships between chlorophytes, chrysophytes, and oomycetes. Proc. Natl. Acad. Sci. U.S.A. 84: 5823–5827.

Hébant, C. 1977. The Conducting Tissues of Bryophytes. J. Cramer, Vaduz.

Hendriks, L., Y. Van de Peer, M. Van Herck, J. M. Neefs & R. DeWachter. 1990. The 18S ribosomal RNA sequence of the sea anemone *An. sulcata* and its evolutionary position among other eukaryotes. Fed. Eur. Biochem. Soc. Lett. 269: 445–449.

Huss, V. A. R. & M. L. Sogin. 1990. Phylogenetic position of some *Chlorella* species within the Chlorococcales based upon complete small-subunit ribosomal RNA sequences. J. Molec. Evol. 31: 432–442.

Källersjö, M., J. S. Farris, A. G. Kluge & C. Bult. 1992. Skewness and permutation. Cladistics 8: 275–287.

Kantz, T. S., E. C. Theriot, E. A. Zimmer & R. L. Chapman. 1990. The Pleurastrophyceae and Micromonadophyceae: A cladistic analysis of nuclear rRNA sequence data. J. Phycol. 26: 711–721.

Kendrick, P. & P. R. Crane. 1991. Water-conducting cells in early fossil land plants: Implications for the early evolution of tracheophytes. Bot. Gaz. 152: 335–356.

Kluge, A. J. 1989. A concern for evidence and a phylogenetic hypothesis of relationships among *Epicrates* (Boidae, Serpentes). Syst. Zool. 38: 7–25.

Lewis, L. A., L. W. Wilcox, P. A. Fuerst & G. L. Floyd. 1992. Concordance of molecular and ultrastructural data in the study of zoosporic Chlorococcalean green algae. J. Phycol. 28: 375–380.

Ligrone, R. & R. Gambardella. 1988. The sporophyte-gametophyte junction in bryophytes. Advances Bryol. 3: 255–274.

Maddison, W. P. & D. R. Maddison. 1992. MacClade: Analysis of Phylogeny and Character Evolution, 3.0. Sinauer Associates, Sunderland, Massachusetts.

Mattox, K. R. & K. D. Stewart. 1984. Classification of the green algae: A concept based on comparative cytology. Pp. 29–72 *in* D. E. G. Irvine & D. M. John (editors), The Systematics of Green Algae. Academic Press, London.

Melkonian, M. 1990. Chlorophyte orders of uncertain affinities: Order Microthamniales. Pp. 652–654 *in* L. Margulis, J. O. Corliss, M. Melkonian & D. J. Chapman (editors), Handbook of Protoctista. Jones and Bartlett Publishers, Boston.

Mindell, D. P. 1991. Aligning DNA sequences: Homology and phylogenetic weighting. Pp. 73–89 *in* M. M. Miyamoto & J. Cracraft (editors), Phylogenetic Analysis of DNA Sequences. Oxford Univ. Press, New York.

Mishler, B. D. 1994. Cladistic analysis of molecular and morphological data. Amer. J. Phys. Anthropol. 94: 143–156.

——— & S. P. Churchill. 1984. A cladistic approach to the phylogeny of the ""bryophytes." Brittonia 36: 406–424.

——— & ———. 1985. Transition to a land flora: Phylogenetic relationships of the green algae and bryophytes. Cladistics 1: 305–328.

———, M. J. Donoghue & V. A. Albert. 1991. The decay index as a measure of relative robustness within a cladogram. Hennig X. Toronto, Ontario. [Abstract.]

———, K. Bremer, C. J. Humphries & S. P. Churchill. 1988. The use of nucleic acid sequence data in phylogenetic reconstruction. Taxon 37: 391–395.

———, P. H. Thrall, J. S. Hopple, Jr., E. DeLuna & R. Vilgalys. 1992. A molecular approach to the phylogeny of bryophytes: Cladistic analysis of chloroplast-encoded 16S and 23S ribosomal RNA genes. Bryologist 95: 172–180.

Miyamoto, M. M. 1985. Consensus cladograms and general classifications. Cladistics 1: 186–189.

O'Kelly, C. J. & G. Floyd. 1984. Flagellar apparatus, absolute orientations, and the phylogeny of the green algae. BioSystems 16: 227–251.

Palmer, J. D., R. K. Jansen, H. J. Michaels, M. W. Chase & J. R. Manhart. 1988. Chloroplast DNA variation and plant phylogeny. Ann. Missouri Bot. Gard. 75: 1180–1206.

Pickett-Heaps, J. D.1979. Electron microscopy and the phylogeny of green algae and land plants. Amer. Zoologist 19: 545 -554.

Rausch, H., N. Larsen & R. Schmitt. 1989. Phylogenetic relationships of the green alga *Volvox carteri* deduced from small-subunit ribosomal RNA comparisons. J. Molec. Evol. 29: 255 265.

Sluiman, H. J. 1985. A cladistic evaluation of the lower and higher green plants (Viridiplantae). Pl. Syst. Evol. 149: 217–232.

———. 1989. The green algal class Ulvophyceae—An ultrastructural survey and classification. Cryptog. Bot. 1: 83–94.

Steele, K. P., K. Holsinger, R. Jansen & D. Taylor. 1991. Assessing the reliability of 5S rRNA sequence data for phylogenetic analysis in green plants. Molec. Biol. Evol. 8: 240–248.

Stewart, K. D. & K. R. Mattox. 1975. Comparative cytology, evolution and classification of the green algae with some consideration of the origin of other organisms with chlorophylls a and b. Bot. Rev. 41: 104–135.

Swofford, D. L. 1991. PAUP: Phylogenetic Analysis Using Parsimony, 3.1. Illinois Nat. Hist. Surv., Champaign, Illinois.

Takaiwa, F., K. Oono & M. Suguira. 1984. The complete nucleotide sequence of a rice 17S rRNA gene. Nucl. Acids Res. 12: 5441–5448.

Theriot, E. 1988. A review of Sluiman's cladistic classification of green plants with particular reference to flagellar data and to land plant origins. Taxon 37: 913–919.

Waters, D. A., M. A. Buchheim, R. A. Dewey & R. L. Chapman. 1992. Preliminary inferences of the phylogeny of bryophytes from nuclear-encoded ribosomal RNA sequences. Amer. J. Bot. 79: 459–466.

Wilcox, L. W., L. A. Lewis, P. A. Fuerst & G. L. Floyd. 1992. Assessing the relationships of autosporic and zoosporic chlorococcalean green algae

with 18S rDNA sequence data. J. Phycol. 28: 381–386.

ZECHMAN, F. W., E. C. THERIOT, E. A. ZIMMER & R. L. CHAPMAN. 1990. Phylogeny of the Ulvophyceae (Chlorophyta): Cladistic analysis of nuclear-encoded rRNA sequence data. J. Phycol. 26: 700–710.

ZIMMER, E. A., R. K. HAMBY, M. L. ARNOLD, D. A. LEBLANC & E. C. THERIOT. 1989. Ribosomal RNA phylogenies and flowering plant evolution. Pp. 205–214 *in* B. Fernholm, K. Bremer & H. Jornvall (editors), The Hierarchy of Life. Elsevier, Amsterdam.

A REEVALUATION OF SEED PLANT PHYLOGENY[1]

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ABSTRACT

Seed plant phylogeny is evaluated using a data set of 46 terminals (taxa) and 103 morphological and anatomical characters. Cladistic analyses using the criterion of parsimony were performed on the complete data set as well as on subsets of the data, e.g., excluding fossils and/or combining various complex taxa into single terminals. The results support the placement of the cycads as the sister group of a monophyletic group that includes several fossil "seed ferns" as well as extant *Ginkgo*, conifers, gnetopsids, and angiosperms. When fossils were included, Bennettitales (cycadeoids) were part of an "anthophyte" clade that included gnetopsids and angiosperms. *Pentoxylon* was a sister taxon to the core anthophyte clade, in some, but not all, of the most parsimonious trees. *Caytonia* was not found to be closely associated with the anthophyte clade, but instead was often associated as a sister taxon of the glossopterids, and these two taxa were consistently outside of the *Ginkgo*–conifer–anthophyte clade. In all most parsimonious trees for all analyses, *Ephedra* was to the outside of a clade that included all angiosperm taxa, *Gnetum*, and *Welwitschia*, thus rendering the traditional gnetopsid clade paraphyletic. New information is provided on the morphology of *Caytonia* and some previous interpretations of homology of the caytonian "cupule" are rejected. The effects of sampling, compartmentalization, and polymorphism are explored in these data, showing how different results may be obtained when polymorphic or "summary" terminals are used. The need for more work on gnetopsids and fossil taxa is suggested.

INTRODUCTION

In recent years, several phylogenetic analyses of seed plants have been published, some with explicit emphasis on the relationship of angiosperms to other seed plants (Hill & Crane, 1982; Crane, 1985; Doyle & Donoghue, 1986a, b, 1987, 1992; Loconte & Stevenson, 1990). We refer the reader to Loconte & Stevenson (1990) for a summary and comparison of the results of several of these studies. In this paper we present a new cladistic analysis of seed plant phylogeny based on morphological characters. Unlike the Loconte and Stevenson analysis, our analyses include several fossil taxa as terminals, as did the analyses by Crane (1985) and Doyle & Donoghue (e.g., 1986a, b, 1987).

This study encompasses two major goals. The first, and most obvious, is to provide a character analysis of seed plants, followed by a cladistic analysis and a phylogenetic interpretation of those results. While we feel that we have provided some new insights, a few new characters, and what we feel are more neutral codings (i.e., fewer phylogenetic hypotheses encoded) of some previously used characters, we fully expect readers to focus most intently on the topologies of the cladograms that we present. While this is understandable, our position is that at present all seed plant analyses, whether they are morphological or molecular, are highly preliminary, and suffer from numerous problems. Thus, the second, and we feel most important goal of this paper, is to discuss and evaluate the numerous problems encountered in such broad analyses, show the effects of some of these problems, and propose some solutions, or at least partial solutions, to some problems. However, the overriding message that we wish to convey is that most of the problems associated with such analyses have not been adequately dealt with to this point. The solutions to problems associated with large-scale analyses of diverse taxa may require additional theoretical advances as well as vast improvements in computer hardware and software capabilities. In particular, the inability to analyze efficiently data sets that are larger than a few score taxa forces users to "compartmentalize" analyses, which may result in solutions that are not globally parsimonious (Nixon & Carpenter, in press).

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Materials and Methods

Sampling

Fossil taxa were selected for inclusion on the basis of availability of published or original data, and whether or not we had confidence in proposed reconstructions based on separate fossil organs. Wherever possible, we checked characters as used in previous analyses against original descriptions and revisions in the literature, and in some cases we reinvestigated fossil morphology when material was available (e.g., *Caytonia*, some bennettitalean taxa). These investigations resulted in differences in some character codings relative to previous studies. These differences are discussed below in the section describing fossils, and in Appendix A, which treats all characters used in the analyses.

Extant taxa were sampled to ensure representation of major seed plant groups. Within angiosperms, taxa were selected to represent broad variation and to ensure representative sampling of groups that have previously been hypothesized to be morphologically similar to hypothetical primitive angiosperms. For example, *Magnolia* (Magnoliaceae) represents the traditional Besseyan view (Bessey, 1897) of the primitive angiosperm, *Ceratophyllum* (Ceratophyllaceae) the first branch in various morphological (Les, 1988) and *rbc*L analyses, and *Chloranthus* (Chloranthaceae), *Piper* (Piperaceae), and the monocots the possible basal groups (e.g., Burger, 1977, 1981). The "Amentiferae," considered basal in the "Englerian" view, were represented by *Chrysolepis* (Fagaceae), *Betula* (Betulaceae), and *Casuarina* (Casuarinaceae). *Drimys* (Winteraceae) represents the modified Besseyan hypothesis of Cronquist (e.g., 1981) and others, and *Calycanthus* (Calycanthaceae) the "first branch" of the morphological analyses of Loconte & Stevenson (1991). Other angiosperm taxa were included in an effort to represent major groups and provide connecting structure among the other terminals; e.g., *Platanus* and *Hamamelis*, based on previous analyses, appear to be reasonably placed between the "higher hamamelids" (Fagaceae, Betulaceae, Casuarinaceae in our analyses; see Nixon, 1989) and the lower hamamelids (e.g., *Trochodendron*, *Tetracentron*) and magnoliids. Because we wanted to combine our data with existing *rbc*L data in a separate project (Albert et al., 1994), sampling decisions were further restricted a priori by the availability of *rbc*L data for taxa in our analyses.

The "complete" data set included all taxa (46 terminals) and characters (103) as presented in Table 1. Following the convention of Henning86, characters are numbered starting with character 0. The majority of characters (80) were binary; of the remaining 23 multistate characters, 15 were treated as nonadditive (unordered) and eight were treated as additive (ordered), as discussed in Appendix A.

In addition to the complete data set, several modified data sets were also constructed and analyzed. These included data sets that had certain terminals or groups of terminals excluded completely, and/or groups of terminals "condensed" into single terminals. Terminal condensations were automatically generated in the matrix editor DADA (DADA386 ver. 0.87, Nixon, 1993b). The "strict" condensation option of DADA was selected, in which the new generated "condensed" terminal was scored as polymorphic (*) for all characters that would be polymorphic (variable within the original terminals within the group). DADA translates polymorphic cells to ambiguous (−) upon submission to the Hennig86 daughter process, but retains the polymorphic coding (*) in the working matrix. Terminal exclusions were also automated through the DADA-Henning86 interface, assuring accuracy by retaining a single master copy of the complete data matrix.

The data sets generated by the above procedures included numerous combinations that we are not reporting here because of space limitations. The results that we report here are based on the following five matrices:

I. Complete analysis: 46 taxa, 103 characters; 23.61% ambiguous, of which 1.36 are polymorphic (ambiguity 17.51% excluding 11 within-angiosperm characters, 92–102).

II. Fossils excluded: 31 taxa, 97 characters; 12.31% ambiguous, of which 0.32% are polymorphic (ambiguity 7.69% excluding 11 angiosperm characters, 92–102).

III. Single angiosperm terminal: 29 taxa, 83 characters; 21.77% ambiguous, of which 1.93% are polymorphic.

IV. Fossils excluded, single angiosperm terminal: 14 taxa, 66 characters; 6.61% ambiguous, of which are 3.59% polymorphic.

V. Fossils excluded, single angiosperm and conifer terminal: 9 taxa, 57 characters; 17.8% ambiguous, of which 1.54% are polymorphic.

Note that the number of informative characters for reduced data sets varies. No characters were removed or recoded other than for the condensed terminals. Differences in number of characters used reflects the reduced variation when taxa are removed and/or condensed. Thus, some characters are excluded that vary only among terminals that

TABLE 1. Data matrix. Characters 0–59. ? = unknown; – = inapplicable; . = uncertain homology; * = polymorphism. All treated as missing data.

```
                          0    5    10   15   20   25   30   35   40   45   50   55
                          |    |    |    |    |    |    |    |    |    |    |    |
Aneurophyton              000?010001000-???0000??0?0-0-*0???00?00-00?0000-0-?-?--0?---
Archaeopteris             000?110011210-???000000000-0-0000?0010002000000-0-000--0?-?-
Lyginopteris              0.0?110000210-???000000011110000000?000.100000-0-000--0????
Medullosaceae             0.0?210000210-???200000011110*000000???0.101010-0-000--0????
Callistophyton            010?100000210-???10000001.11000?00000000003101110-10000--0011?
Corystosperm              01??120001200-???10100001011000000?0010003001110-11000--0????
Lepidopteris              ????????????-???10?0???*111000?0?0010003001110-0-000--0????
Tatarina                  011??????????-???10?00??0111000?0?00?00?30?1110-?????--2????
Glossopterids             010-130101200-???10000000111010?0000.*00.0?1110-110??--2????
Caytonia                  ????????????-????00?0??0.-101010?0010003111110-11000--0????
Williamsoniella           010??????????-????00000?0111000001?1.01102101110-0-1?1100????
Cycadeoidea               010?100100110-???200000111110000001?1.01102101110-0-111100????
Williamsonia              010?100100110-???200000111110000001?0.01102101110-0-1?11?0????
Pentoxylon                011?230011200-???000000001110000-000.00.0001110-0-.00--0????
Cordaites                 011?110111200-???100000000-0-0000000100000011011-10000--00???
Cycadaceae                000022110021O-0002000000111100000000100003001110-0-000--00010
Stangeriaceae             000012110011O-0002000010111100000000100003101110-0-000--00010
Zamiaceae                 0000-21100110-00020000.011110*0000001000310l110-0-000--00010
Ginkgo                    0110130111200-000100000100-0-0000000100131111l0-0-000--00010
Taxaceae                  0110110111200-000?01000102-0--0000001000301011l-0-100--00110
Taxod Cupress             0110110111200-000201*00102-0--0000001*003110111-0-100--00110
Araucariaceae             0110110111200-000201*0010*-0-0000000100030101l1-0-100--00110
Pinaceae                  0110110111200--00201000102-0--0000001001301.111-*0000--00110
Cephalotaxaceae           0110110111200-000201000102-0--0000001000301011l-0-000--00110
Podocarpaceae             0110110111200-00020100010*-0-0000000100130l.111-*0000--00110
Ephedra                   0201130111211000100011010 2-0--00000.01113101100-0-1011110100
Welwitschia               0201130111211000120011010101l100112.01110101110-0-1011111101
Gnetum                    0211120111211000120011010112l100112.11110100100-0-1011001101
Chloranthus               .10113010-1111011110111101121111101O1-1111201*0-0-1110102101
Piper                     .10112010-1111011110010101221101101011011120110-0-1110002101
Winteraceae               0101140101110-0111100001011211011111100111201l0-0-1110102101
Calycanthus               0201130101211111111010010112110110111001112111O-0-1110002101
Eupomatia                 0101120101111111111000010112110110111001212111O-0-1111002101
Magnolia                  0101120101111111111000110112110111111001212111O-0-1111002101
Persea                    0101130101211111111000010112110111117101.120100-0-11.-002101
Nymphaea                  210112010---0-0110100111012211011111100121211l0-0-1111002101
Lilium                    110112010---11111000.1010102110110111011121110-0-1110102101
Dillenia                  0101120101111l?1100000010112110110111101120120O0-1110102101
Caltha                    110112010-1111011000010101221101101111011201200O-1110102101
Trochodendron             0101120101110-0111100001011211111l1.1001112012000-1110102101
Platanus                  0101120101211101100000110122110110211101112012000-1110102101
Hamamelis                 0101140101211101100000110112110110111111212012000-1110102101
Chrysolepis               0101140101201101100000110112110110211111212012010-1110102101
Betula                    0101140101211101100000110112110110211111212012020-1110002101
Casuarina                 0101140101211101100011010210--0110001--1212012020-1110002101
Ceratophyllum             210101010---0-011000100100-0-00--0011001112010O-0-11.--02101
```

TABLE 1. Continued. Characters 60–102.

	60 65 70 75 80 85 90 95 100
Aneurophyton	?----00----------0-00?-0----------
Archaeopteris	?00--00----------?000-00?-0----------
Lyginopteris	?000-0111000010000100100000??0?----------
Medullosaceae	?000-0111000-1010011010O?000???----------
Callistophyton	?000-02110000?-1101001?0?000???----------
Corystosperm	?110002200102O-1100000?1??????----------
Lepidopteris	?1?0-022?010?0-1100000?0??????----------
Tatarina	?1?0-022101O?0-1100000?0??????----------
Glossopterids	?1?0-022*000?0-1000001?0??00???----------
Caytonia	?1?0-02210?0?0-1000001?1??????----------
Williamsoniella	?1?0-0100010?101000?00?1??????----------
Cycadeoidea	?1.0-0100010?10100000011?0???1??----------
Williamsonia	?1?0-0100010?10100000?1?0?????----------
Pentoxylon	?1?0-020000O?0-1001001?1??????----------
Cordaites	?11100200.00?0-110100??0?000???----------
Cycadaceae	0000-0?1100000-1001100100000000----------
Stangeriaceae	0100-011000100-1001110100000000----------
Zamiaceae	0100-011000100-1001110100000000----------
Ginkgo	0100-02.000000-1101000100000000----------
Taxaceae	11?0-020000000-1100001000000101----------
Taxod Cupress	1111?020*00000-1100001000000101----------
Araucariaceae	1111102001O000-1100001000000101----------
Pinaceae	1111102001O000-1100001000000101----------
Cephalotaxaceae	1110002000000-1101000100000101----------
Podocarpaceae	111000200-0000-1101000100000101----------
Ephedra	1110001000101111100000100000101----------
Welwitschia	1110001000101111010000211111111----------
Gnetum	111000100010111100000021111111l----------
Chloranthus	11.0-12.000011020000011101101l0?.--111-1101
Piper	11.0-12.000011020000011111101l0?0--10113112
Winteraceae	11.0-12.110011020000011101101101O000111-000
Calycanthus	11.0-12.010011020000011101101101100011O-000
Eupomatia	11.0-12.110011020000011101101101l.00110-000
Magnolia	11.0-12.010011020010011101101101O000110-000
Persea	11.0-12.010011020000011101101100001101-3101
Nymphaea	11.0-12.110010020000011101101100000011O-000
Lilium	11.0-12.110011020000011111101100001100l3110
Dillenia	11.0-12.*000110200000111011011000010011-000
Caltha	11.0-12.010011020000011101101100001001O-000
Trochodendron	11.0-12.110011020000011101101100l0-0011-010
Platanus	11.0-12.000011020000011101101100010011410l
Hamamelis	11.0-12.010011020000011101101101111001212l
Chrysolepis	11.0-12.010011020000011101101100111001312l
Betula	11.0-12.0100100200000111011011011110001212l
Casuarina	11.0-12.010011020000011101101101.--000121-1
Ceratophyllum	11.0-12.000010?200000111011011000110ll-1100

are excluded in the condensed analyses. For example, characters that are relevant only within-angiosperms (92–102) were operationally excluded from analyses in which angiosperm taxa were condensed into a single terminal.

Additionally, as reported elsewhere (Albert et al., 1994), the complete morphological data set was combined with *rbc*L sequence data. For those analyses, fossil taxa were scored as ambiguous (missing) for all *rbc*L data.

Cladistic analyses were performed on Intel 486 IBM PC compatibles using Hennig86 version 1.5 (Farris, 1988), run as a 16-bit DOS daughter process of DADA386 ver. 0.87. All modified data sets were generated directly within DADA, ensuring that characters were scored identically in all separate analyses. Alternative character optimizations and trees for publication were produced using Clados ver. 1.4 (Nixon, 1993a).

In order to increase the likelihood of finding a complete set of most parsimonious trees (Mickevich & Farris, 1982; Luckow & Pimentel, 1985), taxon order in the larger data sets was pseudorandomly shuffled 100 times using the "autospin" option of DADA (Nixon, 1993b) and directly submitted to Hennig86 using the "mh*" option. Trees were collected from each run, and the final set was analyzed with heuristic branch swapping ("bb*"). The autospin command of DADA automatically removes redundant trees from replicate runs by filtering tree files through the Hennig86 "xsteps u" option. This provides an accurate count of the number of trees found, and allows generation of a consensus tree from all the unique trees generated by replicate runs.

Some of the data sets that were generated by condensing groups had few enough terminals to allow analysis by the "ie*" ("implicit enumeration") option in Hennig86, which guarantees to find the complete set of most parsimonious trees for the data. For these data sets (IV, V), replicate randomized taxon order was unnecessary.

Two non-seed-plant fossils (*Aneurophyton*, *Archaeopteris*) were included in the full data matrix, and trees were rooted between *Aneurophyton* and the remainder of taxa. All analyses were simultaneous (outgroups included without a priori assumptions about topology Farris, 1972, 1982; Clark & Curran, 1986; Meacham, 1984, 1986; Nixon & Carpenter, in press). Because outgroups were treated like all other taxa in the analysis, cladograms were globally most parsimonious for the entire dataset (outgroup + ingroup). The final cladograms were rooted between the outgroup terminals and ingroup. In analyses that excluded fossil terminals, trees were rooted between cycads and the remainder of the extant seed plants, based on the results of the full analyses and previously published analyses (Loconte & Stevenson, 1990). It should be noted that such rootings do not affect the topologies of the trees reported.

Theoretical Considerations

Missing Data

Problems associated with missing data and/or polymorphism have not been discussed extensively in the literature, but interest in this topic has increased in recent years (e.g., Nixon & Davis, 1991). We prefer to separate the concept of missing data from that of missing values or general ambiguity. The former occurs when data are unknown or not collected, and the latter when a cell is scored as a "missing" value for reasons other than missing data, such as uncertain homology or polymorphism. Most currently available computer programs, including Hennig86 (Farris, 1988), PAUP (Swofford, 1991), NONA (Goloboff, 1993), MacClade (Maddison & Maddison, 1992) and Clados (Nixon, 1993a), treat missing data computationally the same during optimization and calculation of tree length, e.g., as if the missing cell had all possible states present. Some programs that search for most parsimonious cladograms (e.g., PAUP and NONA) allow the coding of subset polymorphism (e.g., states 0 and 2 present, but not state 1), while polymorphism must be coded as ambiguous (missing), or equivalent to all states present, in the current version of Hennig86. Although Nixon & Davis (1991) discussed the problem in the context of polymorphism coded as missing data (e.g., for Hennig86), these problems are *not* solved by subset polymorphism coding as is available in PAUP and NONA. Other problems do occur, and it is possible that when polymorphic terminals possess only a subset of possible states, PAUP and Hennig86 may report different tree lengths for the same topology; thus, extensive and correlated polymorphism may not allow Hennig86 to find the most parsimonious trees. However, when such conditions exist, the problems pointed out by Nixon & Davis (1991) are most likely even more severe than the problems associated with coding subset polymorphism as missing, and it is doubtful whether the results of either program would be stable to further analyses of monothetic subgroups of polymorphic taxa. The best solution to this problem is to avoid complex multistate characters and polymorphic terminals as much as possible.

Although it is obvious that high proportions of

missing data introduce uncertainty into analyses, it is not yet clear whether this uncertainty is predictable, how to measure it, or how much missing data is allowable within a particular analysis before the results should be rejected as unreliable. This topic is presently the subject of experimental investigation (Nixon, in prep.). Preliminary results indicate a predictable interaction of missing data and homoplasy; the effect of missing data is accentuated by high levels of homoplasy. Data sets that include numerous fossil taxa often have high levels of missing data as a result of imperfectly preserved fossil organs and the difficulty in determining homology of characters that cannot be investigated equally in all terminals. Thus, recent analyses of seed plant relationships have suffered from high levels of missing data, often in excess of 20% of the total number of cells (e.g., 24% in Doyle & Donoghue, 1986b; 23.6% in our complete analysis, or 17.5% excluding inapplicable states coded as ambiguous for some within-angiosperm characters). In our analyses, the vast majority of cells scored as missing were due to lack of information for fossil taxa; this is reflected in the much lower levels of ambiguous data when fossils were excluded from the analyses. Polymorphism in our analyses was low, ranging from 0.3 to 3.59% of the cells in the various matrices. The highest levels were in those matrices with condensed terminals, because condensations generate polymorphism for each character that varies among the condensed terminals.

COMPARTMENTALIZATION, ARTIFICIAL TERMINALS AND POLYMORPHISM

One of the most serious problems in previous analyses of seed plants has been the treatment of complex, diverse groups as single terminals, which then presents difficulty when these terminals are polymorphic (variable within the group as a whole) for certain characters used in the analysis. Coding terminals as polymorphic or ambiguous for these characters may result in incorrect tree topologies, as pointed out by Nixon & Davis (1991). In some cases, cladograms found when terminals are scored as polymorphic do not include any of the most parsimonious cladograms found when the terminal is subdivided into monomorphic units. The method of coding diverse terminals as single units is in effect "compartmentalization" and constraint of the data (see Maddison et al., 1984). This method of compartmentalization relaxes the application of global parsimony, which accounts for the disparate results obtained when analyses are run simultaneously versus compartmentalized and/or constrained. We present some examples of this problem using various modifications of our seed plant matrices below. Contrary to popular belief, this is a problem whether computer programs accept polymorphic codings or whether polymorphisms must be coded as ambiguous. Wherever possible, we have reduced polymorphism in our data by breaking terminals into units that are monomorphic for each character (Nixon & Davis, 1991).

Compartmentalization may result in equally serious errors, which are more subject to researcher bias, when polymorphic terminals are not coded as polymorphic or ambiguous, but instead are coded as having the "presumed" plesiomorphic state for the group represented by the terminal. In the Doyle & Donoghue (1986a, b, 1987) analyses, angiosperms and some other diverse groups, such as conifers and cycads, were treated as single terminals, and several characters were scored either as polymorphic (in those cases missing because of the computer programs used) or as the presumed primitive state for all angiosperms. Thus, for example, the "angiosperm" terminal in the above analyses was scored as having alternate leaves, bitegmic anatropous ovules, and spirally arranged microsporophylls (= stamens), under the assumption that these states were primitive in angiosperms. On the other hand, other polymorphic characters of angiosperms were scored as missing, or ambiguous, such as presence of vessels. Given these choices in character coding, it is not surprising that the Doyle & Donoghue (1986a, b, 1987) analyses did not find a close relationship of angiosperms to Gnetales (with opposite leaves, single integuments, orthotropous ovules, whorled microsporophylls, and foraminate- or simple-plated vessel elements). In order to avoid such bias, we have sampled several angiosperm taxa for observed characters, instead of presuming an angiosperm ancestral form that predisposes placement of angiosperms in our cladograms. Of course, such an approach has other problems, mostly due to potential undersampling (see Nixon & Wheeler, 1991), but we consider these problems to produce less bias than does the practice of designating ancestral states for polymorphic terminals.

HOMOLOGY DECISIONS

One of the most serious problems in any broad cladistic analysis of higher level taxa is the problem of homology assessment among highly divergent taxa. Typically, the more closely related taxa are, the easier such assessments of homology may be.

Seed plant analyses of necessity include taxa with disparate morphology of reproductive and vegetative structures. Some uncertainty exists in homology assignment for some taxa for almost every character in the analysis. For instance, whether angiosperm flowers are compound strobili, and whether carpels are "megasporophylls" are just a few of the problems encountered in an analysis of seed plants. In order to avoid decisions that are laden with phylogenetic hypotheses, we have attempted to code characters based as much as possible on direct observation of features. Whether or not we have succeeded or failed in this effort will be left to the judgment of the reader, and undoubtedly some will vehemently argue that complex models *should be* incorporated into the analysis. An example of such a complex model used by previous authors is the "cupule" of *Caytonia*, which has been coded as homologous with the second integument of angiosperms and Bennettitales by some previous authors (Crane, 1985; Doyle & Donoghue, 1986a, b, 1987). We discuss our interpretation of this structure, both in terms of coding and in terms of our cladistic results, in greater detail below.

Included Taxa

See Table 1 for a list of taxa and the complete data matrix.

FOSSIL TAXA

Fossil taxa were selected for inclusion in our analyses on the basis of availability of data, i.e., completeness of fossils or presumed reconstructions, and relevance to the problem of seed plant phylogeny. While numerous angiosperm fossils are now known, relatively few are complete enough or different enough from modern taxa to be relevant in a broad seed plant analysis (see Crepet et al., 1991, for a review of fossil flowers). Thus, we have not included any angiosperm fossils in our analyses. The descriptions of key fossil taxa below are not intended to be complete, but they emphasize interpretations of fossil characters that differ from previous analyses (e.g., Crane, 1985; Doyle & Donoghue, 1986a, b, 1987, 1992). Sometimes the differences in interpretation are based on new information, either from recent literature or direct reinvestigation (e.g., our reinvestigation of the "cupule" of *Caytonia*). Other differences reflect reinterpretation based on the same data available to other workers; in such cases, we hope that we have simplified interpretations and made them less dependent on a priori phylogenetic hypotheses, but of course such character interpretations of fossils are always open to debate. In cases where we have interpreted certain homologies in fossil taxa differently from authors of previous analyses, we discuss these differences in some detail in both the discussion of characters and the discussion of the fossil taxa. We also have changed some of the terminal units in the analyses in line with recent fossil discoveries so that there is less character polymorphism in the terminals. In these instances we have provided more detailed descriptions of the fossils in conjunction with establishing new terminal units.

FOSSIL PROGYMNOSPERMS

Aneurophyton. Aneurophyton is typically included in phylogenetic analyses of the seed plants as an outgroup terminal, and we follow this tradition here. Other Aneurophytales, such as *Tetraxylopteris* and *Rellimia*, are better known but apparently more derived in certain characters, e.g., planation of reproductive structures (Bonamo & Banks, 1967; Bonamo, 1977, 1983), and should be included in future analyses. *Aneurophyton* is characterized by three-dimensional branching systems with helical (or possibly sometimes decussate) arrangement of lateral branching, protostelic stems, considerable development of secondary growth, and terminal, fusiform sporangia (Serlin & Banks 1978). Stems include a multilobed strand of mesarch primary xylem surrounded by pycnoxylic secondary xylem and tracheids with bordered pits. The ultimate appendages are three-dimensional, two- or three-times dichotomizing branchlets that are often considered to be homologous with the leaves of more recent progymnosperms. There is some variability in reproductive structures in Aneurophytales, with some taxa having aggregate fertile lateral branches that demonstrate a tendency toward planation as well as appearing to be somewhat circinate (e.g., *Tetraxylopteris*). In *Aneurophyton germanicum* Krausel & Weyland the fertile ultimate branchlets dichotomize once, and the two branchlets curve inward and bear two rows of fusiform sporangia on the inner surfaces. All Aneurophytales that have sufficient preservation have been found to be homosporous (Taylor & Taylor, 1993).

Archaeopterids. Archaeopteris is commonly considered to be a composite genus (reconstructed from more than one fossil) that includes frondlike branching systems and trunks of varying size. It is a historically significant genus because it ultimately was the basis of the concept of "progymnosperms." Beck (1960) was able to associate the

coniferous secondary wood of the trunks (*Callixylon*) with frondlike planate branching systems (*Archaeopteris*) based on similar anatomical details. The stem has a eustele of mesarch vascular bundles with pycnoxylic secondary wood having distinctive bands of circular bordered pits on the radial walls of the tracheids (e.g., Beck, 1960). Carluccio et al. (1966) demonstrated that the ultimate branching systems of planate, variously dissected webbed leaves, were actually spirally arranged on all orders of branching. This supported the interpretation that *Archaeopteris* had planate lateral branching systems and not fronds as originally thought. Anatomical studies by Beck (1971) and Scheckler (1978) have refined further our understanding of *Archaeopteris* morphology, anatomy, and ontogeny and have demonstrated that branches originated from axial primordia and not from axillary buds.

Various hypotheses link the Archaeopteridales to taxa with large frondlike leaves (the "cycadophytes") based on presumed homology of the lateral planate branching system with fronds, as well as to simple-leaved branch systems in coniferophytes (Meeuse, 1963; Beck, 1971). More recently, Rothwell (1982) has suggested an alternative origin of conifers from *Callistophyton*-like ancestors based on common pollen structure and platyspermic ovules, among other characters.

Reproductive structures of *Archaeopteris* are fusiform sporangia borne adaxially in rows along terminal fertile leaflike appendages that are terminally dichotomous (e.g., Beck, 1971). *Archaeopteris* species are considered to be either homosporous or heterosporous, and it has been suggested that as fossil taxa become better known all species will be discovered to have been heterosporous (Phillips et al., 1972). Megasporangia may be larger (Arnold, 1935), or smaller (Phillips et al., 1972) than the microsporangia. Fertile ultimate branches are borne helically on penultimate branches that are arranged in planate branching systems. Devonian seeds on branching systems have been associated with *Archaeopteris*-like plants (Arnold, 1935).

FOSSIL SEED PLANTS

Lyginopterids. Lyginopteris has been treated in most previous cladistic analyses of seed plants as a composite taxon (reconstruction) based on several independently described fossil taxa. These include petrified or compressed eustelar stems (*Lyginopteris*), petrified ovules (*Lagenostoma*) within lobed campanulate cupules (*Calymmatotheca*), compressed fronds (*Sphenopteris hoeninghausii* Sternberg), and several types of microsporangiate organs (*Crossotheca*, *Telangium*, *Telangiopsis*, and *Feraxotheca*) that are pinnate and laminar with abaxial sporangia in *Crossotheca* and *Feraxotheca*, but terminal in *Telangium* and *Telangiopsis* (compression fossils with the characteristics of petrified *Telangium*). Stems, leaves, and cupules have distinctive capitate epidermal glands (used by Oliver & Scott, 1904, to recognize the "seed ferns"). Stems have anastomosing radially elongate bands of fibers in the outer cortex (Oliver & Scott, 1904). There is considerable variability within the family Lyginopteridaceae as it is usually circumscribed (Stidd & Hall, 1970; Taylor & Millay, 1981; Galtier, 1988) and relationships within and outside of the family will be better understood as new fossil evidence becomes available. In our analyses we have used a broad composite profile for the lyginopterids as our terminal, but anticipate that in future analyses this terminal would be divided into subunits based on observed variation within the group.

Some previous analyses have interpreted branching in *Lyginopteris* as axillary as opposed to dichotomous (Galtier & Holmes, 1982). We interpret the branching pattern of the lyginopterids as dichotomous, but with occasional close dichotomies that superficially mimic axillary branching (see Taylor & Millay, 1981). We do not know of any definitive evidence of axillary branching in this group. At any rate, because of the diversity within the group, it is possible that some taxa referred to as lyginopterids had dichotomous branching while others had axillary branching, or a mixture of both forms of branching. Thus, we have scored our lyginopterid terminal as unknown for the presence or absence of axillary buds/branching.

Medullosans. Medullosans are characterized by their large bifurcate fronds, complicated but fundamentally eustelar stem anatomy, large noncupulate ovules, and complex synangia (Stewart & Delevoryas, 1956; Millay & Taylor, 1979; Taylor & Taylor 1993; Stewart & Rothwell, 1993). They are commonly preserved as compressions and petrifactions and their vegetative and reproductive anatomy and morphology have been carefully and extensively studied (e.g., Delevoryas, 1955; Stewart & Delevoryas, 1956; Millay & Taylor, 1979; Taylor, 1965, 1971; Taylor & Eggert, 1969; Eggert & Rothwell, 1979; Mapes & Rothwell, 1980; Stidd, 1981, 1990; Dufek & Stidd, 1981; Rothwell & Eggert, 1986), although complete suites of vegetative and reproductive characters are not known for all of the petrified stem taxa. Interpretations

of the stem anatomy and the origin of the synangiate prepollen organs have been subjects of considerable controversy (Eggert & Rothwell, 1979; Rothwell & Eggert, 1986; Stidd, 1990) and there is variation in key vegetative characters within the genus as it is presently circumscribed. *Medullosa endocentrica* Baxter (Baxter, 1949) appears to have a different growth habit (vine vs. tree) and mode of branching (it is the only medullosan with axillary branching; Hamer & Rothwell, 1988). We have encoded the characters of medullosans with treelike growth habit that do not have axillary branching. In future analyses, pending availability of characters, we will add the axillary branching medullosans as an additional terminal unit. Our coding of characters has not been affected by controversies over the origin of the polystelic stem of medullosans or about the homology of the large and complex pollen-bearing organs.

Callistophyton. The Callistophytaceae were first recognized and circumscribed by Delevoryas & Morgan (1954) when they demonstrated that petrified axes superficially similar to *Cordaites* were actually very similar in morphology to the stems of *Lyginopteris.* The vegetative and reproductive anatomy and morphology have subsequently been carefully described. Stidd & Hall (1970) were able to demonstrate the association between ovules of the genus *Callospermarion* (Eggert & Delevoryas, 1960) and fronds of *Callistophyton.* Subsequent studies by Rothwell (1972a, 1975, 1980, 1981) have made the genus one of the best known of the Paleozoic pteridosperms.

Callistophyton is reconstructed as a shrubby plant with spirally arranged fronds with axillary branches and occasional adventitious roots at the nodes. Synangia and ovules were borne on the abaxial surfaces of pinnules. Ovules were not borne in cupules and were platyspermic with the nucellus free from the inner integumentary layer except at the base. Synangia consisted of a ring of laterally fused elongate sporangia. Pollen-bearing organs include *Callandrium* (Stidd & Hall, 1970) and *Idanothekion* (Millay & Eggert, 1970). Pollen in these organs and pollen found in the micropyles of *Callospermarion*-type ovules is of the *Vesicaspora* type, monosaccate with a distal sulcus and two lateral lobes. The pollen is often well preserved and has been found with an intact branched pollen tube (Rothwell, 1972b) and with apparently intact microgametophytes within the walls (Millay & Eggert, 1970, 1974) that are similar to those in extant conifers. These similarities have led to speculation about the relationship between the Callistophytaceae and cordaites and even conifers (e.g., Rothwell, 1982; Stewart & Rothwell, 1993). This is one of the questions best answered in a phylogenetic context and we address the possibility of a callistophytacean–conifer relationship below.

Cordaites. Cordaites constitutes a conspicuous group of plants in many Late Paleozoic floras of the Northern Hemisphere. The earliest descriptions of cordaites were based on the large strap-shaped or lanceolate leaves of *Cordaites* and associated wood and reproductive organs from Europe (Feistmantel, 1876; Grand-Eury, 1877; Renault, 1879). Subsequently, a number of new cordaitalean taxa have been established from other areas and incorporated in three distinct families: Cordaitanthaceae (Cordaitaceae), Rufloriaceae, and Vojnovskyaceae (Meyen, 1984, 1988). The Cordaitanthaceae include Euramerican taxa, while the two other families are based on Angaran forms. There is considerable structural variation among members of the three families, particularly regarding the reproductive organs. The Euramerican cordaites are better understood than the Angaran forms because of abundant petrified material. Reviews of taxa included in the three families were given by Meyen (1988) and Rothwell (1988). The Cordaitanthaceae include wood (*Cordaixylon, Mesoxylon*), pith casts (*Artisia*), roots (*Amyelon, Stelastellara*), leaves (*Cordaites*), male and female cones (*Cordaitanthus*), male cones (*Gothania*), seeds (e.g., *Cardiocarpus, Mitrospermum, Samaropsis*), and pollen (*Felixipollenites, Florinites, Sullisaccites*). There appear to be at least two groupings of taxa: the *Cordaixylon–Cordaites–Cordaitanthus–Florinites–Cardiocarpus* complex, considered in the present study, and the *Mesoxylon–Cordaites–Gothania–Felixipollenites/Sullisaccites–Mitrospermum* complex, but there are other groupings not yet fully understood (e.g., Rothwell & Warner, 1984; Trivett & Rothwell, 1985, 1988; Rothwell, 1988).

The cordaites were tall, profusely branching trees or smaller trees or shrubs (Rothwell & Warner, 1984), with eustelic, pycnoxylic wood and spiral phyllotaxis. Stems of *Cordaixylon* are endarch, while those of *Mesoxylon* are mesarch. Secondary xylem pits are araucarioid (e.g., Renault, 1879; Scott, 1912; Rothwell & Warner, 1984; Trivett & Rothwell, 1985). The pith is conspicuous, typically with a septation of parenchyma tissue.

Foliage comprises large strap-shaped, spatulate or narrow grasslike leaves (*Cordaites*), and at least in some species also small scale or needlelike leaves around buds, at the base of branches or extending

along the branches (Rothwell & Warner, 1984; Rothwell, 1988). There is no mid-vein in *Cordaites*, but numerous, densely spaced, dichotomizing veins that run almost parallel in the leaf lamina.

A detailed account of the organization and structure of the microsporangiate and ovulate cones of *Cordaitanthus* was given by Florin (1950, 1951). The pollen-bearing and seed-bearing cones are similar in basic form; they are compound, and consist of lateral branches borne on a central bracteose axis, either in a planate pattern or spirally arranged. Each lateral branch has a number of spirally arranged scalelike sterile appendages interspersed with sporophylls. These are simple, laminar, with an apical cluster of four to six free microsporangia. Dehiscence is by longitudinal slits toward the center of the sporangial cluster. Pollen grains found in situ in *Cordaitanthus* are similar to dispersed grains assigned to *Florinites*. They are eusaccate, monosaccate, and inaperturate (Florin, 1936; Millay & Taylor, 1974). Male gametophytes were observed in the pollen first by Renault (1902) and later described in detail by Florin (1936). Four to five or six nuclei are arranged in a single row oriented towards the distal pole.

The megasporophylls are stalklike, and in the more recent forms are simple, bearing a single, terminal ovule (*C. zeilleri* Renault), or in the older forms dichotomous, bearing two ovules (*C. pseudofluitans* Kidston). Dispersed and petrified seeds associated with *Cordaitanthus* are assigned to *Cardiocarpus*. The ovules are platyspermic with a single integument consisting of an inner sclerotesta and an outer sarcotesta. A single vascular strand enters the ovule and gives rise to one pair of vascular bundles that pass up through the integument and another pair of vascular bundles that pass into the nucellus. The nucellar cuticle is distinct and free from the integument and thick megaspore membrane.

The microsporangiate cone, *Gothania*, associated with *Mesoxylon*-type wood (Hirmer, 1933), is similar to the compound cone of *Cordaitanthus* in general structure, but differs in having sporangia arranged in a single row at the apex of the sporophyll. Pollen grains found in situ in *Gothania* are eusaccate and monosaccate, with a distinct proximal trilete scar, similar to dispersed pollen of the *Felixipollenites* or *Sullisaccites* type (Millay & Taylor, 1974; Trivett & Rothwell, 1985). Ovules of *Mitrospermum* are linked to *Gothania* by the presence of *Felixipollenites* pollen in the micropyles (Taylor & Taylor, 1993). They are similar to *Cardiocarpus* in most features, but the integument vasculature forms a characteristic tracheal plate, and nucellar vasculature is lacking (Taylor & Stewart, 1964).

Glossopterids. The glossopterids, the signal group of the Gondwana flora, are based on an imprecisely understood assemblage of variously preserved fossils including leaves, stems, roots, and a wide range of reproductive structures (e.g., Delevoryas, 1969; Pant, 1977; Schopf, 1976; Gould & Delevoryas, 1977; Retallack & Dilcher, 1981; Pigg, 1990; Taylor & Taylor, 1993). An excellent overview of pre-1985 literature on glossopterids is provided by Crane (1985) and there have been several interesting and significant studies since that time, including analyses of petrified material from Antarctica (Pigg, 1990; Taylor & Taylor, 1993; Pigg & Taylor, 1990, 1993).

The leaves have a multiveined midrib with anastomosing lateral venation that is not hierarchical with respect to vein order diameters (e.g., Pigg, 1990), and our coding of venation reflects this distinction. In this character, the leaves are similar to those of *Sagenopteris* (considered to be the leaf form of *Caytonia*).

There is a great deal of variation in the nature of ovuliferous and pollen-bearing organs. Reproductive structures termed "glossopterid" include seeds or pollen-bearing sporangia on simple or branched stalks subtended by foliar structures, with the stalks variously adnate to the foliar structures; sometimes the seeds are apparently borne directly on the foliar structures. In some petrified ovulate structures, the ovules appear to be completely enclosed by a foliar organ. Within the envelope, the orthotropous ovules are connected by a network of parenchyma cells that might be interpreted as participating in pollination (e.g., Thomas, 1958; Pant & Nautiyal, 1965; Gould & Delevoryas, 1977; Pant, 1977; Taylor & Taylor, 1993). Pollen-bearing organs consist of variously branched axes terminating in clusters of microsporangia that contain bisaccate and apparently quasisaccate pollen (Surange & Chandra, 1975; Gould & Delevoryas, 1977; Meyen, 1987). There has been some uncertainty expressed in the literature about the nature of these reproductive structures (i.e., foliar vs. axillary). Based on the full range of forms, the apparent axillary nature of the seed stalks, and the occurrence of additional opposing bracts in some taxa, we regard these structures as axillary branch systems with variously modified fertile appendages, adnate to a subtending bract. Thus, in encoding the characters for *Glossopteris*, in contrast to pre-

vious analyses (e.g., Crane, 1985), we have interpreted the pollen and ovuliferous structures as axillary and not foliar. The close association of and/or fusion of fertile axillary structures to foliar appendages is consistent with the morphology of reproductive structures in most other seed plants with axillary branching, such as the conifers, *Ginkgo*, and gnetopsids, and is also consistent with some interpretations of the angiosperm carpel/placenta complex. This interpretation of the seeds as borne on axillary structures is suggested by many of the impression specimens of various glossopterids, both ovulate and pollen-bearing. It is also consistent with both our interpretation of, and the recent literature on, other Mesozoic seed fern fertile appendages, such as in corystosperms and peltasperms, as axial systems as opposed to megasporophylls (Taylor & Archangelsky, 1985; *Antevsia*, Friis & Pedersen, in prep.).

Recent discovery and careful analyses of petrified axes of *Glossopteris* provide additional morphological and anatomical characters that have not been available in the past (e.g., alternate (spiral) phyllotaxy; *Araucarioxylon*-like wood; endarch primary xylem; Pigg & Taylor, 1993). Some of these characters (e.g., *Araucarioxylon*-like wood) are shared with certain Mesozoic seed fern taxa (Table 1; Pigg & Taylor, 1993).

The diversity encompassed within the glossopterids, while imperfectly understood at the present time, makes it clear that in future analyses they will have to be divided into more than a single terminal, each based on a specific reconstruction. As discussed below, "summary" taxa are problematic, and such problems are exacerbated with groups such as the glossopterids for which there is minimal if any evidence for monophyly.

Peltasperms. The family Peltaspermaceae was established by Thomas (1933) based on the ovulate fossil *Peltaspermum*, the associated *Lepidopteris* leaves, and the microsporangiate structure *Antevsia* from the Triassic of South Africa, Sweden, and Greenland (Thomas, 1933; Harris, 1937). Subsequently, a variety of dispersed leaves (e.g. *Compsopteris*, *Kirjamkenia*, *Meyenopteris*, *Phylladoderma*, *Tatarina*), pollen-bearing organs (*Permotheca*, *Pterispermostrobus*), pollen (e.g., *Monosulcites/Cycadopites*, *Protohaploxypinus*, *Vesicaspora*, *Vittatina*), ovulate organs (*Autunia*, *Peltaspermopsis*), and seeds (*Salpingocarpus*) have been assigned to the Peltaspermaceae (Gormankov & Meyen, 1986; Meyen, 1987, 1988; Kerp, 1988; Poort & Kerp, 1990). There is considerable variation in structure among the peltasperms, and in the present analysis we consider two groupings of taxa: the Late Permian *Tatarina–Permotheca–Protohaploxypinus/Vittatina–Peltaspermopsis–Salpingocarpus* complex known from the Eurasian Angara flora (e.g., Meyen, 1984; Gormankov & Meyen, 1986; Meyen, 1988) and the Late Triassic *Lepidopteris–Antevsia–Monosulcites/Cycadopites–Peltaspermum* complex known from Greenland, Sweden, and South Africa (Antevs, 1914; Thomas, 1933; Harris, 1937; Pedersen, 1981).

The peltasperms were probably woody plants. A system of short and long shoots with spirally arranged leaves was described for *Tatarina* (Gormankov & Meyen, 1986; Meyen, 1988), but otherwise little is known about habit and growth form and no wood has been identified in association with the *Lepidopteris* plant.

Leaves of *Lepidopteris* have generally been interpreted as bi- or tri-pinnately compound with conspicuous tuberculate bodies and folds along the main rachis (Nathorst, 1886; Antevs, 1914). Schimper (1869), in his original description of the genus, described these folds as scale leaves, while Nathorst (1886) believed that they were merely cuticular expansion over the tubercular bodies that had folded as a result of fossilization. A reexamination of well-preserved material from Scania shows morphology and epidermal patterns suggesting that Schimper's original interpretation is correct (Friis & Pedersen, in prep.) and that the "frond" of *Lepidopteris* should be interpreted as a branch system with the main axis bearing scale leaves alternating with lateral branches borne in a planate arrangement. The lateral branches bear scale leaves as well as larger laminar leaves. The laminar leaves are simple or once-pinnate. According to this interpretation the *Lepidopteris* branch system is comparable to that of an *Archaeopteris* "frond" and branch systems of some conifers. Leaves of *Tatarina* are simple, lobed, or once-pinnate. Gormankov & Meyen (1986) also included fossil leaves with palmately dissected lamina (e.g., *Kirjamkenia*) in the Peltaspermaceae, and dichotomous bipinnate fronds have been observed in several Permian leaves (e.g., *Peltaspermum* (*Callipteris*) *martinsii*, Poort & Kerp, 1990). The cuticle is typically very thick in the peltasperms, and epidermal features may be difficult to study in detail. The venation pattern is open dichotomizing, fan-shaped or pinnate, pinnules typically lacking or having an indistinct mid-vein; the stomata are haplochelic and scattered on both the abaxial and adaxial surface (Antevs, 1914; Gormankov & Meyen, 1986; Poort & Kerp, 1990).

The microsporangiate organs of *Antevsia* associated with the *Lepidopteris* leaves have been interpreted as compound, bipinnate microsporophylls in previous phylogenetic analyses (Crane, 1985; Doyle & Donoghue, 1986a, b, 1987). However, reexamination of specimens from Greenland and Sweden (Friis & Pedersen, in prep.) shows that they are branched structures consisting of a prominent mid-axis with spirally arranged lateral appendages that bifurcate once or twice. The ultimate units are laminar, bearing eight elongate and free sporangia in two rows. Dehiscence is by a longitudinal split opening toward the center of the microsporangiate clusters. Pollen grains found in situ in the microsporangia of *Antevsia* are similar to dispersed grains assigned to *Monosulcites minimus* Cookson or *Cycadopites*. They are monocolpate with a smooth outer surface, thick lamellate endexine, and a thick homogenous ektexine (Pedersen, 1981). The microsporangiate organs of the *Tatarina*-complex are only fragmentarily preserved, and their structure is not fully understood (Zalessky, 1929; Gormankov & Meyen, 1986; Meyen, 1988). The material consists mainly of dispersed clusters of microsporangia, while only a small fragment of an axis was described. The dispersed clusters of microsporangia are similar to those of *Antevsia*, although the laminar unit bearing the sporangia is not very distinct from the illustrations. Each cluster consists of up to possibly eight narrow, free sporangia that are fused only at the base either to each other or possibly to a laminar structure as seen in *Antevsia*. Several different species of *Permotheca* were described based on dispersed microsporangia clusters (Gormankov & Meyen, 1986). Species associated with *Tatarina* leaves contain striate quasisaccate (*Protohaploxypinus*) as well as striate asaccate (*Vittatina*) type pollen (Gormankov & Meyen, 1986; Meyen, 1987). *Protohaploxypinus* type pollen was also discovered in situ in the seeds of *Salpingocarpus bicornutus* Gormankov & Meyen and *Vittatina* type pollen in the seeds of *Salpingocarpus variabilis* Gormankov & Meyen (Gormankov & Meyen, 1986). A *Permotheca* species producing *Vesicaspora* is associated with *Phylladoderma* (Gormankov & Meyen, 1986; Meyen, 1988).

The ovulate organs (*Peltaspermum* and *Peltaspermopsis*) consist of a main axis bearing stalked peltate and radially symmetrical discs in a spiral arrangement. The ovulate organs assigned to these two genera are distinguished mainly on the basis of the associated leaves, and Poort & Kerp (1990) indicated that when treated as a form genus, *Peltaspermopsis* should be included in *Peltaspermum* (see also Durante, 1992). In the Triassic *Peltaspermum*-type organs the discs are widely spaced, while in some of the Permian forms (e.g., *Peltaspermopsis*), they form dense heads. Ovules were borne along the lobed margin of the discs. Those associated with *Lepidopteris* are apparently unitegmic with a bent, simple micropylar tube and a free nucellus (Harris, 1932a), but their organization is not fully understood. There are no details on the seeds attached to Permian forms associated with *Tatarina*, but the dispersed seeds of *Salpingocarpus* are believed to be produced by *Peltaspermopsis* (Gormankov & Meyen, 1986). *Salpingocarpus* is described as being platyspermic and unitegmic with the nucellus free from the integument and with a distinct salpinx. The nucellar membrane is thin and closely adheres to the thick megaspore membrane. In *S. bicornutus* the integument at the micropylar area is bifid, while in other species of *Salpingocarpus* the micropylar area is simple (Gormankov & Meyen, 1986).

Corystosperms. The Corystospermaceae are a predominantly Gondwanan group of plants first described by Thomas (1933) based on the ovulate structures of *Umkomasia* and *Pilophorosperma*, the associated dispersed seeds of *Spermatocodon*, microsporangiate structures of *Pteruchus*, and leaves of *Dicroidium* from the Middle Triassic of South Africa.

The discovery of *Dicroidium* leaves attached to *Dadoxylon*-type stems from the Middle Triassic of Antarctica documents a woody habit for at least some corystosperms (Meyer-Berthaud et al., 1992). Previous studies have indicated a possible relationship between *Dicroidium* and *Rhexoxylon* type wood in other parts of Gondwana (South America and South Africa) based on common association and presence of secretory cavities (Archangelsky & Brett, 1961; Archangelsky, 1968). It is possible that several wood types were present in the corystosperms. The leaves (*Dicroidium*) are once-pinnate with dichotomizing mid-vein (e.g., Thomas, 1933; Townrow, 1962; Anderson & Anderson, 1983).

The microsporangiate structures of *Pteruchus* consist of a central axis with stalked lateral appendages, each unbranched and terminating in a laminar-peltate structure bearing 20–100 abaxially arranged sporangia. The sporangia are free and dehisced by a longitudinal slit (Thomas, 1933; Townrow, 1962). A spiral arrangement of the lateral units was illustrated for several specimens of *Pteruchus* by Thomas (1933) and further de-

scribed for material from India (Pant & Basu, 1979), which indicates a branching system rather than a foliar nature for *Pteruchus*. Pollen grains are quasisaccate or eusaccate (Taylor et al., 1984; Yao et al., 1992; Zavada & Crepet, 1985).

The ovulate structures of *Umkomasia* and *Pilophorosperma* are compound branching systems consisting of a central axis with lateral branches arising in the axils of bracts. The branches are apparently arranged in one plane (e.g., *U. polycarpa* Holmes) or are spiral (e.g., *U. sessilis* Holmes) (Holmes, 1987). One to several pairs of stalked or more rarely sessile ovulate units are borne along the lateral branches, the distal pair being distinctly bifurcate, while bifurcation may also account for the paired position of the more proximal ovulate units, but this is less clear. Thomas (1933) described bracteoles subtending the ovulate units in some of the South African specimens, but such bracteoles were not observed in the Australian material described by Holmes (1987). Each ovulate unit consists of an outer recurved and cup-shaped envelopment enclosing a single ovule. The ovule is small with a slightly bent and bifid micropylar tip. It has been described as platyspermic, but no permineralized specimen has been described so far.

Thomas (1933) originally described the fertile structures of *Umkomasia* as branching systems. His interpretation was based on ovulate material in which the lateral appendages were subtended by distinct bractlike structures. The axillary nature of the lateral appendages in *Umkomasia* was later documented by Holmes (1987) from the study of well-preserved specimens from Australia. Bracts were not observed in the microsporangiate structures, and Townrow (1962) interpreted this as an indication of a foliar nature for both the ovulate and the pollen-bearing structure. This view was followed by Crane (1985) and Doyle & Donoghue (1986a, b, 1987), who characterized the fertile structures as being compound pinnate sporophylls. However, the recent discovery of permineralized fragments of *Pteruchus* showing radially symmetrical vascular bundles of the central axis indicates a branch system with spirally arranged lateral units for the pollen-bearing organs (Yao et al., 1992). In our analyses we therefore interpreted the reproductive structures of both sexes as branching systems, not sporophylls.

Caytoniales. Caytonia was originally described as an angiosperm by Thomas (1925). The association of characters that he interpreted as angiospermous included, most notably, a fleshy saclike structure with a stigmalike lip, which enclosed several seeds, possibly in two rows. Pollen grains were found on the "lip," and strands of cuticle extending from the lip to the seeds were taken as remnants of pollen tubes (Thomas, 1925). Later authors have referred to the saclike seed-enclosing structure of *Caytonia* as a "cupule," but care should be taken in using this term until the homology of the structure is more clearly established. The "cupules" of *Caytonia* are arranged along an axis (as interpreted by Thomas) or the rachis of a leaf (as interpreted by some other authors, discussed in detail below).

Caytonia has become an informal name for a composite taxon based on an association of organ genera that includes leaves (*Sagenopteris*), synangiate pollen-bearing organs (*Caytonanthus*), and seed-bearing structures (*Caytonia*; Figs. 1, 2). Similarities in cuticular structure among *Sagenopteris* petioles and both *Caytonia* and *Caytonanthus* axes were noted by Thomas (1925, 1933). Pollen in synangia matches pollen in seed micropyles (e.g., Harris, 1964), and these organ genera are consistently associated at various localities (e.g., Thomas, 1925, 1933; Harris, 1932b, 1940, 1941; Lundblad, 1948; Reymanówna, 1973). Thus, there is considerable evidence that these organs represent the same taxon.

The pollen-bearing organs of *Caytonanthus* are synangiate with 3–5 sporangia and, according to Thomas, are borne on the apparently abaxial surface of pinnate microsporophylls (Thomas, 1925; see also Harris, 1941). Leaves are palmately compound with apparent net venation (Thomas, 1925). Some years later, Harris (1933) published an analysis of new specimens of *Caytonia*, in which he demonstrated pollen in the micropyles of seeds and on that basis refuted the angiospermous nature of Caytoniales. Thomas (1925), Harris, and recently Reymanówna (1973), have made detailed studies of *Caytonia* and more recently, pollen has been studied (Pedersen & Friis, 1986; Zavada & Crepet, 1986).

Although Thomas's original interpretation of *Caytonia* as an angiospermous plant has been rejected by most subsequent authors, efforts have persisted to associate *Caytonia* and the angiosperms based on other interpretations of homology. Such conclusions are based chiefly on an evolutionary model proposed by Gaussen (1946), who interpreted the second integument of angiosperm seeds as homologous with the "cupule" of *Caytonia*. Under the Gaussen model, evolutionary reduction from several seeds to one seed within the incurved "cupule" of *Caytonia* would give rise to an anatropous, bitegmic ovule, as is found in many angiosperms. The "cupule" of *Caytonia* would then

be homologous with the "second" or outer integument of some angiosperms, cycadeoids, and under some interpretations, *Pentoxylon*. The Gaussen model has been directly encoded in the data matrices of some recent cladistic analyses of seed plants (e.g., Crane, 1985; Doyle & Donoghue, 1986a, b, 1987, 1992); along with such encodings, the angiosperms have been treated as a single terminal scored as having anatropous, bitegmic ovules. Encoding such phylogenetic hypotheses, both in terms of the model of transformation and the presumed ancestral state of angiosperms, biases cladistic analyses in such a manner that the results may falsely confirm the original model.

We have reinvestigated material of *Caytonia*, *Caytonanthus*, and *Sagenopteris* in order to better understand the nature of these organs and in particular the caytonian "cupule." Our reinvestigation is based on direct observation of numerous specimens (on loan to W. Crepet from the University of Connecticut Paleobotanical Collection) of all three genera collected at Cayton Bay by Henry N. Andrews and Maurice Wonnacott and prepared by Henry N. Andrews. We have verified features of leaf venation for *Sagenopteris*, sporangial characters for *Caytonanthus*, and we present here the results of scanning electron microscope (SEM) examination of various new preparations of *Caytonia* (Figs. 1, 2). Indeed, our direct reexamination has revealed certain characteristics that have not been published previously and raises questions about some of the features reported by other workers working only with light microscopy (LM).

The *Caytonia* "cupule" or seed envelope is fleshy, saclike, and preserved in various orientations (Fig. 1A, B), often with an attached stalk or "pedicel" (Fig. 1B). The envelope has a proximal stoma with a lip adjacent to the "pedicel" or stalk (Fig. 1B) and encloses 8–10 flattened seeds (Fig. 1C, D), arranged with the micropylar ends oriented toward the center and lip (Fig. 1A). Whether the seeds are attached in more than one row is still uncertain, as is the nature of the vasculature that feeds the seeds, even after examination with both LM and SEM. The inside of the envelope is largely composed of spongy parenchymatous cells, and internally there is no detectable smooth epidermis.

The recurved lip of the envelope (Fig. 2A) is apparently laterally continuous with the pedicel; there is no indication of an envelope wall between the pedicel and stoma, and therefore it appears that the adaxial surface of the pedicel forms the wall of the stoma opposite the lip. This interpretation is reinforced by the papillose nature of the epidermis of the recurved "lip" of the cupule, which intergrades proximally and laterally with the epidermis of the adaxial pedicel (Fig. 2A, B, C). In well-preserved specimens the recurved "lip" can be observed to have channels in the papillose epidermal cells that may have provided access into the interior of the otherwise sealed envelope (Fig. 2A, B). In some cases these channels apparently occur also in the epidermis of the proximal "lip" formed by the adaxial pedicel (Fig. 2B). Our studies of *Caytonia* cupules failed to confirm the tubes/strands first observed by Thomas (1925) and later by Reymanówna (1973) connecting the micropyles of the ovules with the channels in the recurved external lip of the envelope (Fig. 2A, B). We did observe surface channels in the interior walls of the cupules flanked by rows of large parenchymatous cells (Fig. 1B, C) that are possibly continuous with the external channels and might also have appeared to be tubes in the preparations of Reymanówna (1973) and Thomas (1925). It is also possible that their material was better preserved or differently prepared from our material.

Another interesting feature of the Cayton Bay specimens is an apparent residue of preserved solute extending between the lip of the cupule and the proximal pedicel epidermis (Fig. 2C, D). This may be the remnant of solute rich liquid (for which a preservational precedent exists in the pollenkitt observed in Cretaceous in situ angiosperm pollen by Friis et al., 1988) and suggests the possibility of a pollination drop mechanism (as is known for several extant gymnosperms) for moving pollen from the outside of the seed envelope to the micropyles of seeds in *Caytonia*. However, in this case, the pollination droplet would be associated with a group of seeds instead of the micropyle of a single seed.

Because of the orientation of the lip and pedicel, we do not interpret the *Caytonia* "cupule" as an anatropous structure in the sense of anatropous ovules of angiosperms. In angiospermous anatropous ovules, the micropyle is formed by the integuments and is found distal to the point of attachment of the funiculus, except in such cases when the funiculus is adnate laterally to the (outermost) integument. If the ovule is inverted (recurved), the ovule is termed anatropous, and the funiculus is either free or is adnate to the second integument. Thus, in angiosperms with anatropous ovules the micropyle is formed by one or both of the integuments; in contrast, in *Caytonia* the stoma of the seed envelope is formed by the wall of the seed envelope (lip) only on one side, and the pedicel forms the other side of the stoma. In *Caytonia* there is no evidence for either a distal attachment

FIGURE 1. SEM preparations of *Caytonia* sp. – A. Fruit compressed dorsiventrally with the pedicel removed, showing the outlines of overlapping seeds. To the right are several folds suggesting a more or less globose form before compression. Scale bar = 0.5 mm, UCPC 6000. – B. A broken fruit with a complete pedicel, showing channels in the large internal epidermal cells and the papillose pedicel epidermis. Scale bar = 0.2 mm, UCPC 6001. – C. A fruit with the abaxial wall removed to show seeds within, apparently borne in two rows and oriented toward the center lip. Note also the channels in the interior epidermis that are more or less continuous with the openings (toward the bottom of the specimen) from the recurved lip-pedicel interface. Scale bar = 0.5 mm, UCPC 6002. – D. Lateral view of the fruit illustrated in C, illustrating the overlapping seeds. Scale bar = 0.5 mm.

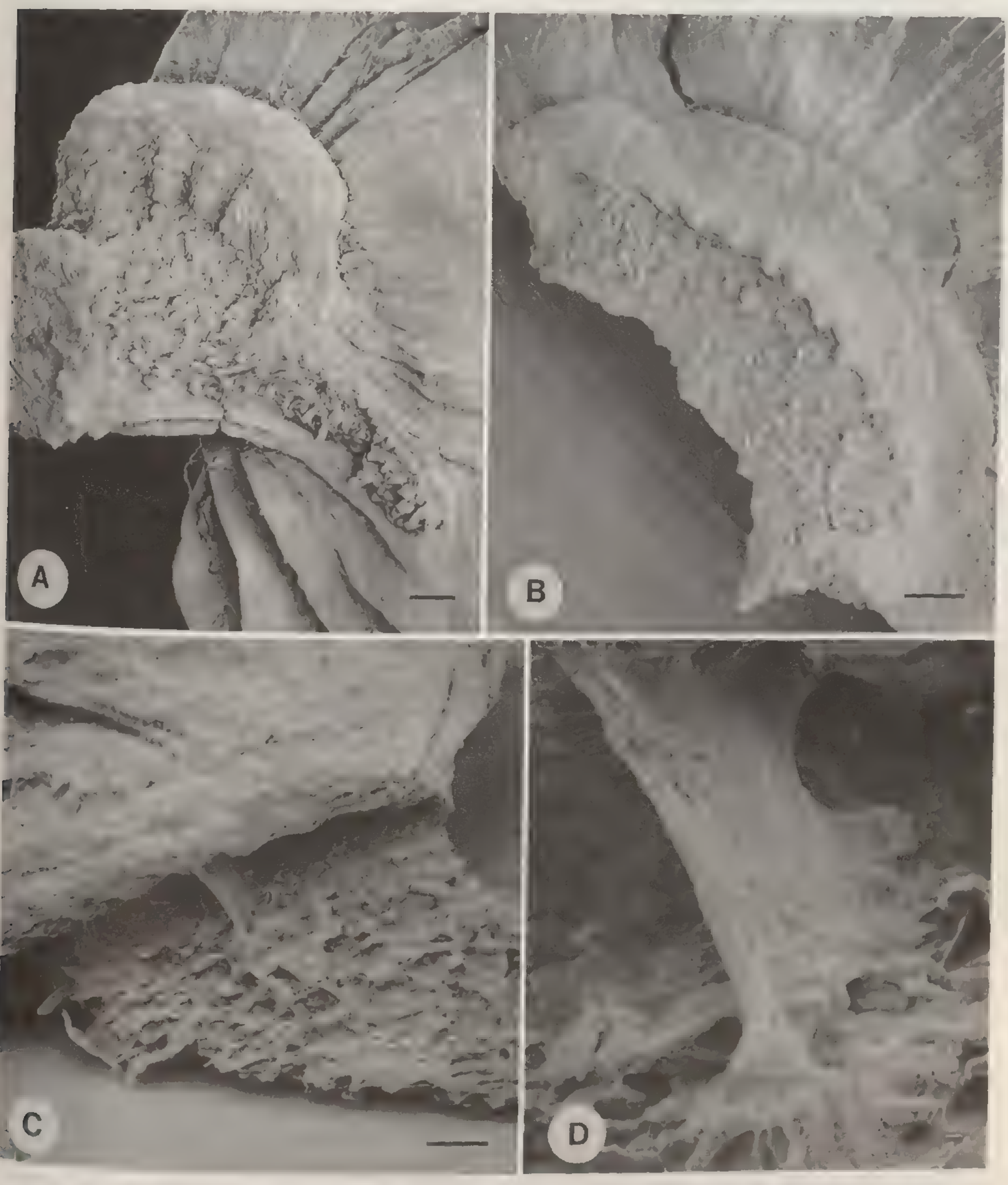

FIGURE 2. SEM preparations of *Caytonia* sp. —A. View of the pedicel-lip interface showing the channels in the recurved lip, the continuity of the lip-pedicel epidermis, and the participation of the adaxial pedicel in the opening into the fruit. Note also the numerous folds in the fossils, again suggestive of its globose nature in life. Scale bar = 0.05 mm, UCPC 6003. —B. The lip of specimen UCPC 6000, illustrating the channels in the lip and the attachment of the recurved lip to the lateral pedicel. Scale bar = 0.1 mm. —C. Lip-pedicel area of UCPC 6001 showing preserved solute that is possibly a remnant of a "pollen drop" or other exudate from lip. Scale bar = 0.05 mm. —D. Higher magnification view of the remains of a pollen drop illustrated in C. Scale bar = 18 μm.

of the stalk or a separate layer that would represent the continuation of the "cupule" (= second integument of authors) between the stalk and stoma. Instead of a structure that is analogous to an anatropous ovule, it appears that the *Caytonia* seed envelope is more similar in form to a planate leaflike appendage that has curved inward upon itself (semicircinate) with connate margins, forming a saclike structure. The seeds that are enclosed might be interpreted as borne directly on the foliar append-

age (envelope), or in our estimation a more consistent interpretation would be that the seeds are borne on an axillary stem system that has become adnate to the subtending bract (envelope). At any rate, given the incurved, not anatropous, nature of the structure, the connation to the stalk, and only partial involvement of the envelope wall in formation of the stoma, it does not appear to be a reasonable precursor of any known ovules with two integuments, much less the specific anatropous bitegmic ovule envisioned by Gaussen (1946). We have encoded the ovules of *Caytonia* as orthotropous and unitegmic, based on observations of their attachment within the "cupule" and the lack of any second layer around each seed. As discussed below, these characters greatly affected the outcome of the analyses of Crane (1985) and Doyle & Donoghue (1986a, b, 1987), and those seeking to evaluate the merits of our results relative to theirs should pay close attention to the treatment of these characters.

Pentoxylon. *Pentoxylon* is considered to be a small tree with strap-shaped leaves, long and short shoots, leaf cushions on the smaller branches, elliptical ovulate heads, and branching microsporophylls that are arranged in a whorl on a rim that subtends a terminal domelike structure (Bose et al., 1985; Crane, 1985). As used in previous cladistic analyses, *Pentoxylon* is a composite Jurassic–Cretaceous taxon based on both association and structural similarities of petrified and compression-based organ genera (Sahni, 1948; Bose et al., 1985; Crane, 1985). These include stems (*Pentoxylon*, Sahni, 1948), leaves (*Nipaniophyllum* for petrified leaves, Sahni, 1948; *Taeniopteris* for compressed leaves identical to those of *Nipaniophyllum*), ovulate heads of various types such as *Carnoconites* (Srivastava, 1946; Bose et al., 1985), and branched pollen-bearing organs (*Sahnia*) that have been variously interpreted (Vishnu-Mittre, 1953; Bose et al., 1985; Taylor, 1988).

Stems (*Pentoxylon*) are basically eustelic (Beck et al., 1982; Stewart, 1976; Crane, 1985; Taylor & Taylor, 1993), but unusual in a way similar to stems of Medullosaceae (Crane, 1985; Taylor & Taylor, 1993). They have up to 16, but most often five or six, triangular wedges of primary and secondary wood in transverse section. The primary vascular bundles are mesarch and are surrounded completely but unevenly by secondary development of pycnoxylic wood with uniseriate rays that are up to seven cells in height and lack ray tracheids (Crane, 1985; Taylor & Taylor, 1993). There is greater development of secondary wood toward the center of the stem, and this uneven development imparts the triangular cross-sectional appearance to each of the vascular units. There is no axial parenchyma, and radial walls have uni- and biseriate round bordered pits. The bundles are separated by parenchymatous areas analogous to rays, and these are confluent with the pith and cortex, both of which have nests of sclerotic cells, but no resin canals (Taylor & Taylor, 1993). There are some specimens with radially aligned cells in the cortex suggestive of periderm (Taylor & Taylor, 1993). Leaf traces arise in pairs, one from each of a pair of vascular traces (Stewart, 1976).

In petrified *Nipaniophyllum raoi*, strap-shaped leaves up to 20 cm in length have an entire margin and a midrib that extends to the apex and consists of several parallel veins. Lateral veins depart from the midvein at right angles (pinnately) and branch occasionally with the branches fusing near the midvein. The petioles are very short and have 5–9 veins matching the number of bundle scars typically found on the leaf "cushions" of the stems (Taylor & Taylor, 1993). The stomata are confined to the abaxial leaf surface and are sometimes oriented in rows. There have been some questions as to the nature of the subsidiary cells. Sahni (1948) originally reported the stomata as similar to those of bennettitalean leaves (presumably syndetocheilic), but Rao (1976) noted that many were apparently anomocytic (and presumably haplocheilic).

Pollen-bearing organs (*Sahnia*) consist of receptacles about 1 cm in diameter with a raised rim bearing a whorl of delicate axes, approximately 2 cm high. The axes have short, spirally arranged appendages (microsporophylls?) that terminate in clusters of two to four, stalked, thick-walled pollen sacs (Vishnu-Mittre, 1953; Taylor, 1988). Vishnu-Mittre (1953) noted that the microsporangiophores were connate at their bases into a shallow cup and were surrounded by deciduous bracts. Rao (1981) later suggested that these microsporangiate structures were actually free at their bases; Bose et al. (1985) concurred. Vishnu-Mittre (1953) reported scalariform tracheid thickenings in the vascular tissue of microsporangiate structures and short shoots of *Sahnia*, but this was later contested by Bose et al. (1985), who observed no such thickenings.

The pollen is monosulcate, about 25 μm in diameter and has a complex exine structure that appears endoreticulate with an inner lamellate layer (Osborn et al., 1991). Monosulcate pollen has been observed in the micropyles of seeds of *Carnoconites* (see Bose et al., 1985; Crane, 1985, 1988; Taylor & Taylor, 1993).

The seed-bearing organs (*Carnoconites*) asso-

ciated with *Pentoxylon* are unique. They are borne terminally on short shoots and may be ovoid-elliptical or more elongate (Srivastava, 1946). The ovules are orthotropous on short stalks and are not subtended by any discernible structures, nor are there any interseminal scalelike structures as found in the ovulate receptacles of the Bennettitales (Bose et al., 1985). Ovulate heads may be arranged at the ends of laterally branched pedicels or multiple pedicels may emanate from the distal short shoot, each terminating in an ovulate head. The ovules are sessile with a single vascular strand and are crowded together so that they appear polygonal (usually rhomboidal) in surface view (Srivastava, 1946). The seeds are somewhat flattened. The two-layered integument is free from the nucellus except at the chalazal end, with an inner bicarinate sclerotesta and outer fleshy sarcotesta. Details of the cuticles are difficult to determine in the petrified material (Sahni, 1948; Bose et al., 1985), but in macerations of compression fossils of *C. cranwelliae* Harris, Harris (1962) noted that the sarcotesta had a thick outer cuticle, there was a robust nucellar cuticle, and that there was no preserved megaspore membrane. Harris also discovered some isolated delicate cuticles "in the bottom of the maceration pot" that he speculated might represent a thin cuticle of the inner surface of the sarcotesta. Crane (1985, 1986, 1988) interpreted this as evidence for two integuments in the seeds of *Pentoxylon*, but, because of the uncertainty of the true nature of these isolated cuticles and due to the difficulty in observing cuticles in intact material, we chose to score integument number as unknown for *Pentoxylon*.

Because of its unusual nature and the many questions that still surround an interpretation of its morphology, *Pentoxylon* is in need of continued investigation.

Bennettitales (Cycadeoidales). The Bennettitales include two families, Williamsoniaceae and Cycadeoidaceae (Taylor & Taylor, 1993). Bennettitales are well represented in Triassic through Cretaceous sediments and include an interesting mixture of fossils that are very well known (e.g., some species of *Cycadeoidea*) and those that are intriguing, and, possibly phylogenetically significant, but imperfectly understood (e.g., *Wielandiella*, Nathorst, 1909; *Leguminanthus* and *Sturiella*, Krausel, 1948; *Westersheimia*). In some instances it is not entirely clear that these taxa are bennettitalean. Recent direct examination of *Wielandiella* type specimens at the Swedish Museum of Natural History (Friis & Crepet, unpublished) revealed that the reproductive structures are not well enough preserved to unequivocally describe; but cycadeoid affinities, suggested by leaf structure, cannot be ruled out, nor can the bisporangiate condition be absolutely ruled out for these cones. In spite of the uncertainty surrounding several taxa, the Bennettitales have been the objects of considerable attention because of the striking characters they share with flowering plants. They were first described in the nineteenth century (e.g., Buckland, 1827, 1828; Williamson, 1870; MacBride, 1893; Lignier, 1894) and became very well known through the work of Wieland (1906), whose demonstration of cosexual strobili in petrified species of *Cycadeoidea* from the Black Hills of the Unites States was heralded as the discovery of a missing link between the angiosperms and gymnospermous ancestors (Arber & Parkin, 1907). This was, at its time, one of the most widely appreciated contributions of the field of paleobotany to the botanical sciences. The complex bisporangiate structures of Bennettitales are additionally interesting because of the structural variation among taxa and evidence of insect pollination in, at least, *Cycadeoidea* (Crepet, 1972, 1974).

Bennettitales are known from compressions of reproductive structures, leaves, and stems, and as petrifications from a wide range of geographical locations including North America, Europe, India, and Greenland (Delevoryas, 1963, 1968; Crepet, 1974; Harris, 1969; Pedersen et al., 1989; Sahni, 1932).

The Bennettitales vary in habit from delicately branched forms without apparent persistent leaf bases (*Wielandiella*; Nathorst, 1909) to more robust, sparsely branching columnar trunks with persistent leaf bases as in *Williamsonia* (Sahni, 1932) to the familiar ovoid or stout columnar, sparsely branching (*Cycadeoidea* and *Monanthesia* (Wieland, 1906; Delevoryas, 1959). Leaf form varies from entire-leaved taxa to variously regular or irregularly pinnate forms. Cone positions also vary within Bennettitales. They may either be exposed at lateral branch terminals and surrounded only by sterile bracts (*Williamsonia*), or be borne terminally and subtended by two lateral branches (*Wielandiella*), or be terminal on short lateral branches that bear cone-surrounding bracts (*Cycadeoidea, Monanthesia*). In the latter instances the short shoots bearing the cones do not extend far enough to elevate the cones beyond the leaf bases that persist on the trunks (*Cycadeoidea, Monanthesia*).

As currently interpreted, reproductive structures in the Bennettitales consist of ovulate recep-

tacles that are fleshy and conical or dome-shaped. They bear hundreds to thousands of orthotropous ovules, sometimes with elongated funicles, among sterile interseminal scales with expanded polygonal apices. Tubular micropyles extend beyond the armored surface defined by the tangential walls of the polygonal heads of the interseminal scales.

Microsporophylls in Bennettitales vary in structure around a pinnate groundplan. Microsporophylls are in a single whorl, which in cosexual cones subtends the ovuliferous portion of the receptacle (*Cycadeoidea, Williamsoniella*). Sporangia are tubular, and enclosed in elongate or kidney-shaped synangia that are often borne in two rows on the microsporophylls (Wieland, 1906; Delevoryas, 1963; Crepet, 1974).

Many bennettitalean taxa are well known and well preserved (*Cycadeoidea*: Wieland, 1906; Crepet, 1974; *Williamsoniella*: Thomas, 1915; and *Williamsonia* spp.: e.g., Sahni, 1932). However, there are fundamental questions that remain unresolved even in some of the well-known genera. The most basic of these involves the equivocal nature of some of the Upper Triassic Bennettitales (Kräusel, 1948), but there is also some question about the actual distribution of bisexual (cosexual) versus unisexual reproductive structures in Bennettitales. The latter is not as simple a question as it may appear to be. In *Cycadeoidea*, differential maturation times of the pollen and seed-bearing organs led to the assumption that some species were unisexual when they were not, even in well-preserved and carefully examined petrified specimens (Crepet, 1974). Some well-preserved members of Cycadeoidaceae are still relatively poorly understood (e.g., *Monanthesia*) in this regard because they have not been thoroughly investigated. Equivocally identified Bennettitales are, in general, poorly understood, so the association of male and female reproductive structures is far from clear in these taxa. Nonetheless, it does seem unlikely that any of them could have been cosexual. In *Vardekloeftia*, the best known of the Triassic taxa with respect to the ovulate receptacle, the ovulate receptacles were apparently attached by slender stalks and have therefore been presumed to be unisexual (Pedersen et al., 1989). Perhaps the best evidence for unisexual Bennettitales is in the Williamsoniaceae. Several species of *Weltrichia*, a form genus for the compressed microsporangium, appear to have been dispersed without ovulate parts. The variously modified pinnate microsporophylls are fused basally into cups that apparently contain no ovulate receptables (e.g., *Weltrichia spectabilis* Nathorst; *W. whitbiensis* Nathorst; Nathorst, 1911). In some specimens, however (*W. santalensis* Sitholey & Bose, Sitholey & Bose, 1971), the nature of the fossil suggests the possibility that these microsporophylls had dehisced from a relatively broad cylindrical axis as might be expected if they subtended an ovulate receptacle.

Recent analysis of relationships within the Bennettitales have suggested that the group is basally unisexual (Crane, 1988). This finding is congruent with the fossil record of Bennettitales if one excludes *Wielandiella* as too poorly understood to be unequivocally bisexual (and we concur) and if one includes other poorly documented, but apparently unisexual, Triassic taxa in the analysis. Crane's (1988) analysis used *Pentoxylon* as the outgroup and included a complete suite of bennettitalean fossils, but no other seed plants. Many of these taxa, of necessity, had a relatively high number of missing values.

With respect to Bennettitales, our analysis differs from previous broad seed plant analyses in the explicit taxa (reconstructions) we included instead of treating the group as a single terminal, and in our coding of several characters. The use of explicit reconstructions helped us avoid the necessity of scoring the group for presumed ancestral states or as ambiguous states for polymorphisms, as was done by Doyle & Donoghue (1986a, b, 1987). On the other hand, we excluded many bennettitalean taxa for two related reasons: (1) too much uncertainty about their structure or affinities to unequivocally score characters (e.g., equivocally bennettitalean or particularly poorly understood fossils, *Wielandiella*, Nathorst, 1909; *Leguminanthus*, Kräusel & Schaarschmidt, 1966; *Sturiella*, Kräusel, 1948; *Westershiemia*, Kräusel, 1949; *Bennetticarpus*, Harris, 1932b); (2) inclusion of particular poorly known taxa would excessively elevate levels of missing data within terminals. In our initial analyses, we made an effort to include *Vardekloeftia*, but because of limited data we could only score the terminal for approximately 30% of the characters used in our analysis. Thus, *Vardekloeftia* was excluded from our final analyses because it generated massive numbers of cladograms resulting in deresolved consensus trees by uniting with too many disparate groups (for a discussion of this phenomenon, see Nixon & Wheeler, 1991).

We differ from Crane (1988) in our interpretation of the distribution of the corona within the Bennettitales. In contrast to Crane (1988) we code *Cycadeoidea* as having a corona. The anatomical details of the corona, as an apical extension of the ovulate receptacle, are only well understood in *Cycadeoidea*. However, some species of *Cycad-*

eoidea do not have coronas (those with dome-shaped and small ovulate receptacles); our reconstruction and character coding for *Cycadeoidea* is based on *C. dakotensis* Ward. There is a possibility that the corona of *Cycadeoidea* is not homologous with the coronas of the other corona-bearing taxa (e.g., *Williamsoniella*), but this cannot be evaluated until more is known about the structure of the corona in a range of taxa within the order. In *Cycadeoidea*, the corona is not a fleshy extension of the ovulate receptacle, but is made of apparently elongated modified interseminal scales that have elongate cells with spiral thickenings similar to those found in transfusion tissue in conifers (Crepet, 1974). The nature of the tissue composing the corona in *Williamsoniella* is unknown (Thomas, 1915). Another complication is that the "corona" may be more widespread than is known because it will not be detected in petrified material unless the longitudinal section is very close to median (thus, it is difficult to rule a corona out in some species of *Williamsonia*).

It is interesting to note that modified interseminal scales similar to those making up the corona of *Cycadeoidea* are also found at the bases of the ovulate receptacles. It is possible that these areas are modified for conduction of substances that might be associated with pollinator attraction/rewards.

EXTANT TAXA

Cycads. The Cycadales are treated here as three terminals: Cycadaceae, Stangeriaceae, and Zamiaceae. Such a treatment is preferable to a single cycad terminal because it reduces the level of polymorphism and allows more parsimonious constructions of ancestral states within the cycad clade based on observed patterns, not ideal character combinations (Nixon & Davis, 1991). Because of the relatively low diversity of the cycads, and the nature of the characters used in our analyses, we were able to treat the cycad (and conifer) terminals as summary taxa (characters scored for whole monothetic groups) as opposed to exemplar samples, as we were forced to do with angiosperms. The phylogenetic analyses of Stevenson (1990, 1992, 1993) support each of the three cycad families used in our analyses as monophyletic. No fossil cycads were included in our analyses, and the scores assigned to the three cycad terminals are based solely on observation of characters in extant taxa. This treatment differs from that of Doyle & Donoghue (e.g., 1992) who, for example, scored their single cycad terminal as having simple leaves based on the presumed cycadalean affinity of a simple-leaved fossil. The affinity of many presumed fossil cycads with extant families is uncertain or at best equivocal.

Conifers. As with the cycads, the extant conifers were not treated as a single terminal but rather as several terminals along familial delimitations to avoid excessive scoring of polymorphisms. The selected terminals (Araucariaceae, Cephalotaxaceae, Pinaceae, Podocarpaceae, Taxaceae, and Taxodiaceae–Cupressaceae) are consistent with classical family limits as well as the results of recent cladistic analyses (Hart, 1987; Miller, 1988) at the generic level, although the interfamilial relationships obtained by Hart (1987) and Miller (1988) are quite disparate. The inclusion of Taxodiaceae and Cupressaceae in a single terminal as circumscribed by Eckenwalder (1976) is supported by the results of both Hart and Miller. Our intent is not to produce a complete analysis within conifers, and any conclusions on familial relationships within the conifer clade are tentative.

Gnetopsids. The three extant genera of gnetopsids (*Ephedra*, *Gnetum*, and *Welwitschia*) were treated as separate terminals in all of our analyses. Because our analyses resulted in trees in which these taxa did not form a monophyletic group, we did not analyze any data sets in which the three genera were fused into a single terminal. Particular interpretations of characters for gnetopsids are discussed below and in Appendix A.

Angiosperms. The full data set included 18 angiosperm terminals. These were scored in our matrix for characteristics of the genera represented by these terminals (i.e., states for larger inclusive groups such as families were not extrapolated). The sampling strategy is outlined above. In some analyses, the 18 angiosperm terminals were condensed into a single "angiosperm" terminal, which was scored as polymorphic for all characters that varied among the original 18 terminals.

CHARACTERS

The 103 characters used in our "complete" analysis include vegetative and reproductive morphology, anatomy, and palynology. The discussion below focuses on instances where we have departed from the scoring and/or use of characters in recent studies of seed plant phylogeny, particularly those of Loconte & Stevenson (1990) and Doyle & Donoghue (1992). Several "new" characters have been added in our analyses, and we have scored differently several characters that have been used in previous analyses. In some cases, the differences

from previous treatments involve corrections of errors or the addition of new information, either published or from our reinvestigation of certain fossil taxa.

Unless otherwise noted, all multistate characters have been treated as nonadditive (= unordered). For exceptions, see Appendix A.

Obviously, there is a vast amount of literature available as a source of characters and states for particular taxa. Fortunately, there are also extensive and seminal compendiums of this literature. These works have made the extraction of data much easier and we owe a great deal to our predecessors. Among the more important of these for our study are the works of Bierhorst (1971), Chamberlain (1935), Crane (1985, 1988), Cronquist (1981), Martens (1971), Meyen (1987), Gifford & Foster (1988), Singh (1978), and Taylor & Taylor (1993). Unless otherwise stated, the source of character data can be assumed to be from these works; as much as possible, we have examined the primary references found therein, as will often be apparent by the citations in Appendix A and in the section describing fossils above.

Results of Cladistic Analyses

I. COMPLETE ANALYSIS

Several tree "islands" were found based on randomized spins of taxon order with DADA386 and Hennig86. There were a total of 834 equally parsimonious trees of length 339, retention index (RI) 0.78, and consistency index (CI) 0.38. The strict consensus of these cladograms is presented in Figure 3. A representative tree selected from among the most parsimonious trees is presented in Figures 4–6, with characters mapped. Portions of two other trees are presented in Figures 7 and 8 to illustrate variable positions of *Ginkgo*, *Pentoxylon*, and other seed ferns. If only the extant taxa are considered, the pattern is similar, but not identical, to that found by Loconte & Stevenson (1990), with the cycad clade as a sister group of the remainder of extant seed plants, and the conifer clade as a sister group of gnetopsids + angiosperms, as illustrated in Figures 5 and 8. Important features of the consensus tree include the lack of a monophyletic gnetopsid group and the position of *Ginkgo*, which in some trees (e.g., Figs. 4, 8) is outside of the conifer clade + anthophytes, and in other trees (e.g., Fig. 7) is a member of a broader "conifer" clade. The "higher" or Mesozoic pteridosperms are highly unresolved in the consensus, forming a large polytomy that includes *Ginkgo* as well as the conifer and "anthophyte" clade. Some of the relative placements of taxa contributing to this polytomy are illustrated in Figures 4, 5, 7, and 8, with characters mapped to illustrate character support.

II. FOSSILS EXCLUDED

When fossils were excluded, six most parsimonious trees were found, with CI 0.47 and RI 0.79. No tree islands were noted. The consensus of these trees is presented in Figure 9, rooted to the cycads to facilitate reference to the full analysis. The consensus is highly resolved, with polytomies occurring only within the angiosperm clade. *Chloranthus* is consistently the "first" branch of the angiosperms, with *Ceratophyllum* the next branch. The within-angiosperm topology is consistent with a subset of the trees found in the full analysis. Outside the angiosperm clade, the only differences in topology from that of the full analysis are the position of *Ginkgo*, which when fossils are excluded is outside of the conifer clade in all most parsimonious trees, and the more complete resolution within the extant conifers, with Podocarpaceae as the first branch.

III. SINGLE ANGIOSPERM TERMINAL

When the 18 angiosperm terminals are condensed into a single terminal using the "fuse terminal" option of DADA386, six trees of length 196 (188 excluding autapomorphies), CI 0.50, and RI 0.75 are found. The consensus of these trees is presented in Figure 10. In contrast to the complete analysis, the position of *Ephedra* relative to the other gnetopsids and angiosperms is stabilized, with Bennettitales to the outside. The pteridosperm taxa, which were unstable and joined in a large polytomy in the complete analysis, now show a very stable topology, in which *Pentoxylon* is associated with the "anthophyte" clade as a first branch, and the remainder fall to the outside of the *Ginkgo*–Conifer–anthophyte clade. In these trees, *Caytonia* and the glossopterids always form a monophyletic group.

IV. FOSSILS EXCLUDED, SINGLE ANGIOSPERM TERMINAL

When the fossils were excluded from the data set in analysis III, with a single condensed angiosperm terminal, only one tree of length 110, CI 0.78, and RI 0.85 was found. This tree (Fig. 11) is identical in topology to those found in analysis II (fossils excluded). If only extants are considered, it can be seen that it differs from analysis III (angiosperms condensed) only in having resolved the relative position of Podocarpaceae and Cephalotaxaceae within the conifer clade.

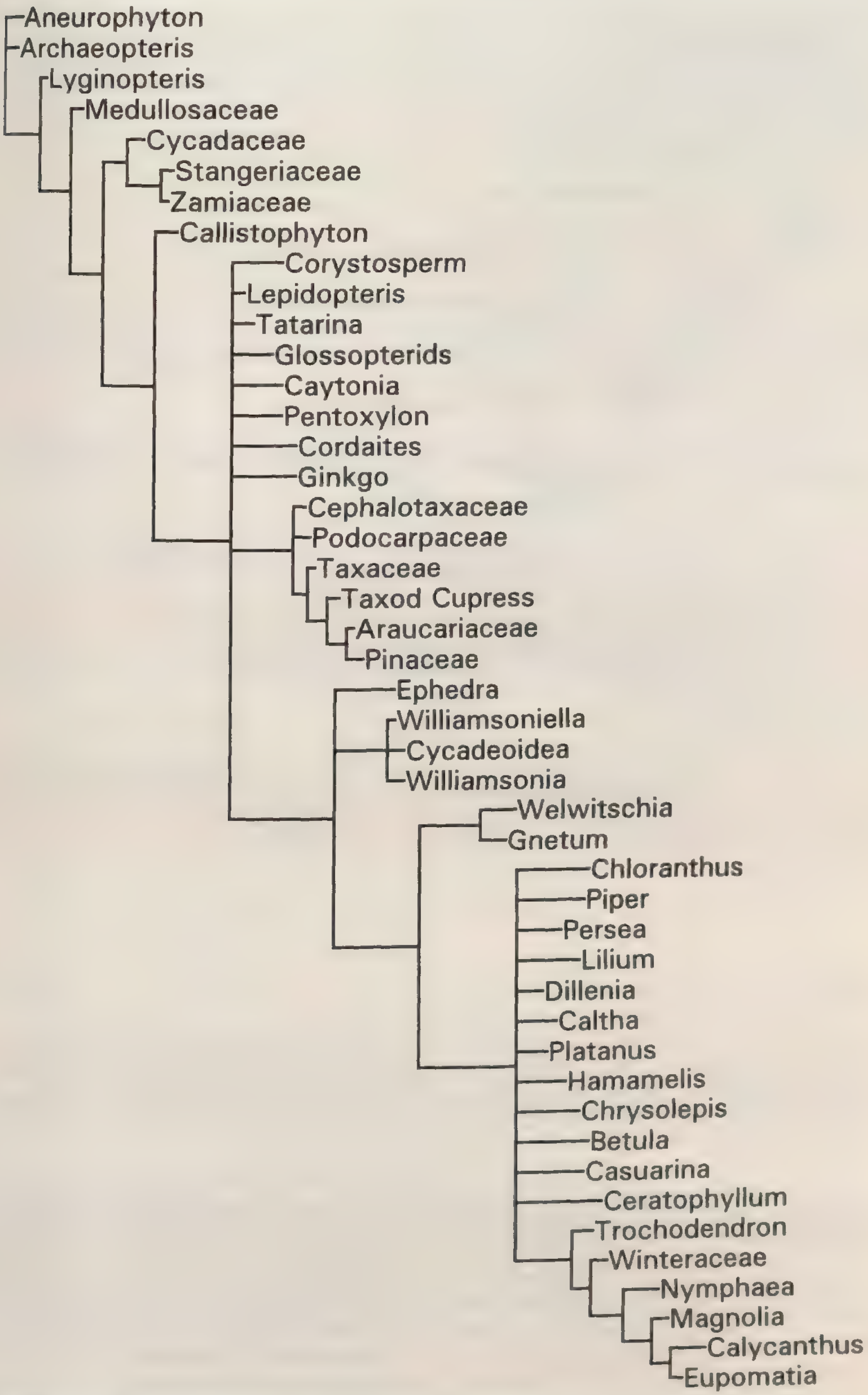

FIGURE 3. Strict consensus of most parsimonious cladograms found for matrix I (full data set).

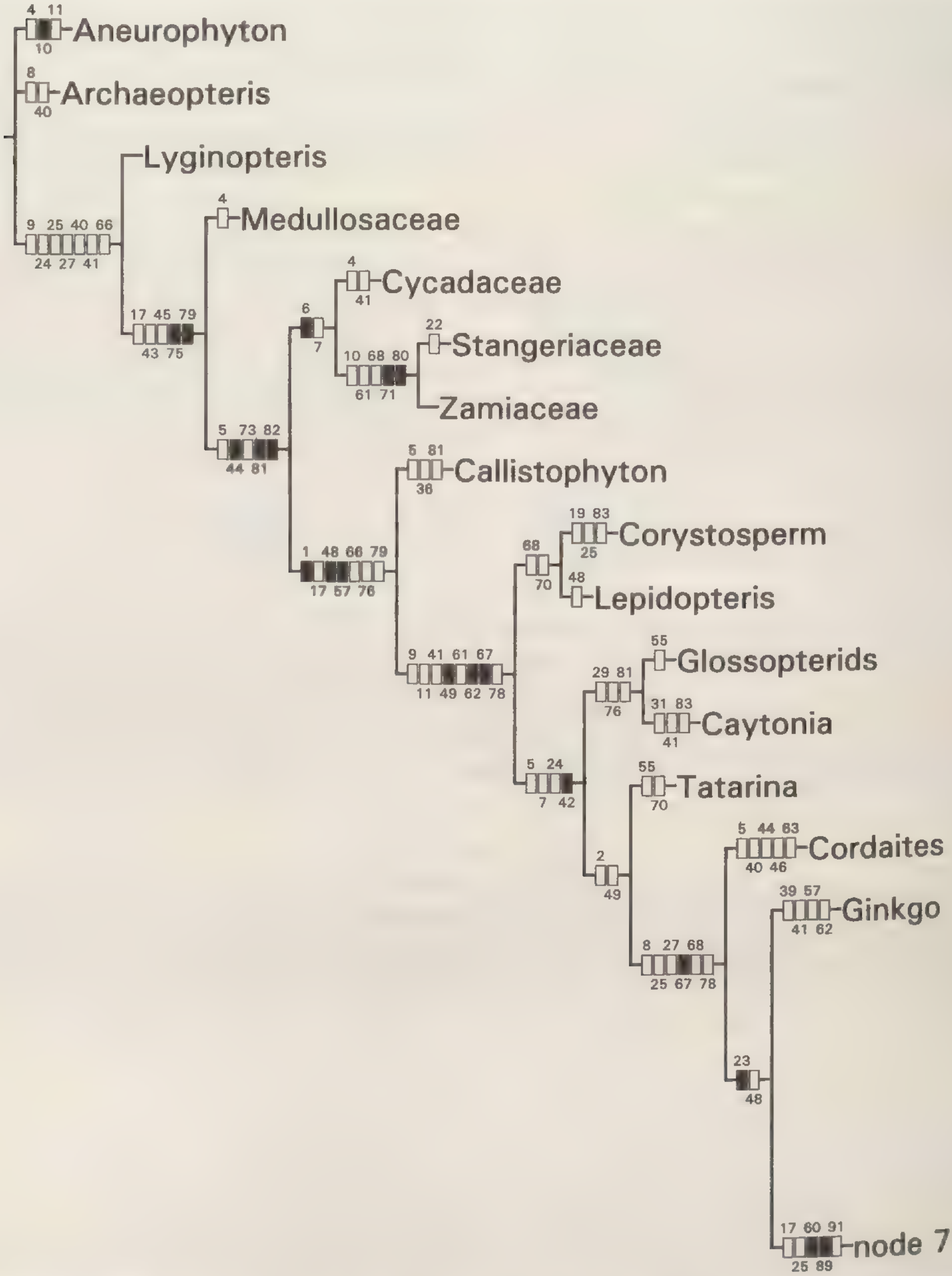

FIGURE 4. Basal section of one of the most parsimonious trees found for matrix I (full data set). Characters are numbered above and below hashmarks. Optimization is arbitrary in some cases where alternative character states may occur at nodes, but length of tree is correct regardless of optimization. Solid black hashmarks represent unique origins of states; open hashmarks represent states not derived uniquely under the optimization presented.

V. FOSSILS EXCLUDED, SINGLE ANGIOSPERM AND CONIFER TERMINALS

Condensing the conifer terminal in addition to the angiosperm terminal, and analyzing the matrix with fossils excluded resulted in only two trees of length 97, CI 0.85, and RI 0.87. The consensus of these two trees is presented in Figure 12. The two trees differ only in whether *Ginkgo* is outside of the conifer clade + anthophytes, or is on the conifer clade. Thus, when only extants are considered, this analysis produced the same two topologies as were found in the complete analysis.

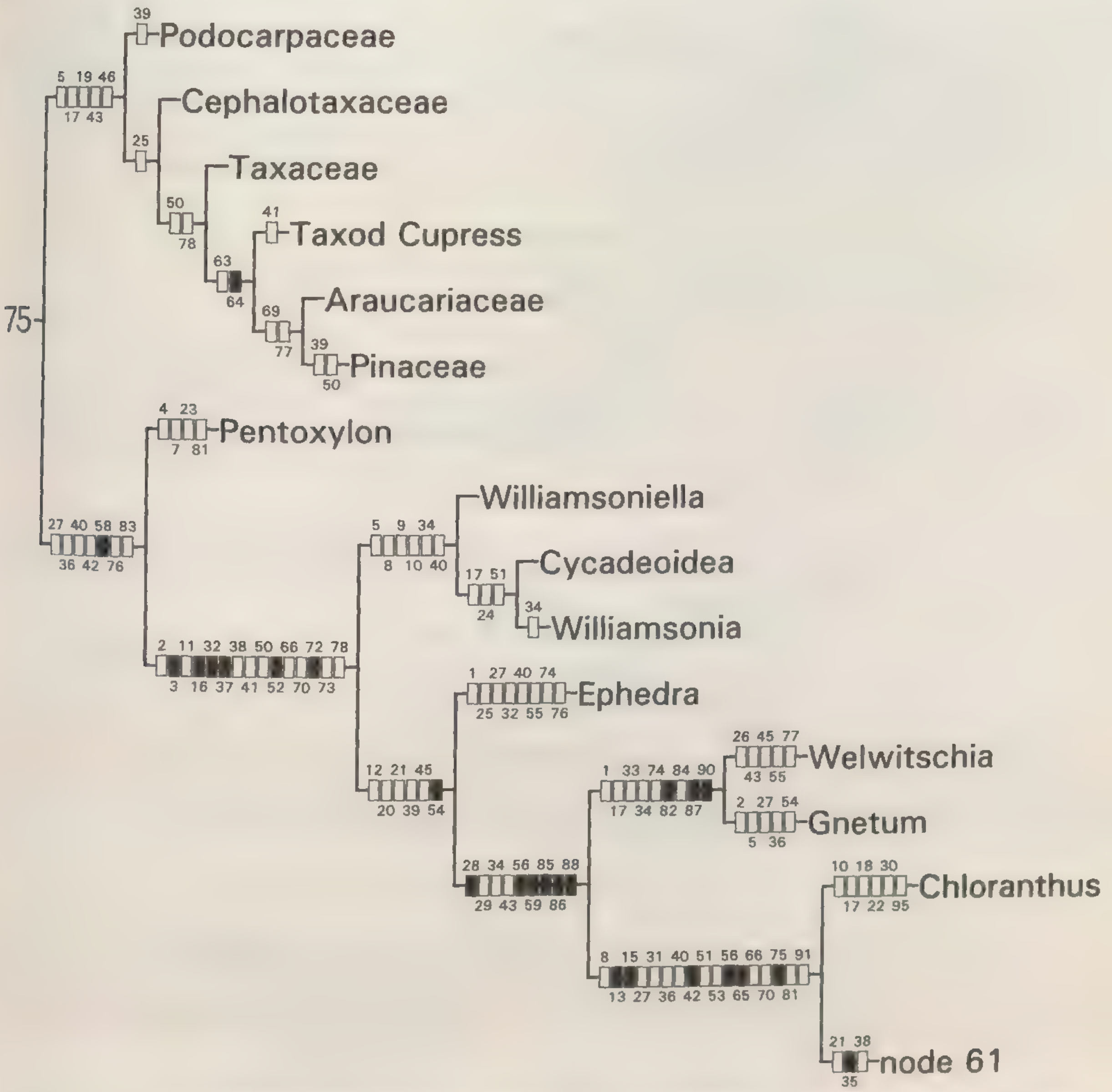

FIGURE 5. Middle section of tree in Figure 4, one of the most parsimonious trees found for matrix I (full data set). Hashmarks as in Figure 4.

DISCUSSION

The general pattern of our results for extant taxa conforms most closely with the previous results of Loconte & Stevenson (1990), particularly in the placement of the cycad terminals relative to *Ginkgo*, the conifers, and angiosperms. Considering only extants, in the complete analysis, *Ginkgo* was either a sister group of the conifers, or of a clade that included conifers, gnetopsids, and angiosperms. The latter is the only topology found by Loconte & Stevenson (1990), and by us in the remainder of our manipulations (excluding fossils, collapsing angiosperm and conifer clades to single terminals). Based on our results and those of Loconte and Stevenson, we favor recognition of a "ginkgophyte" group that includes *Ginkgo*, conifers, gnetopsids, and angiosperms. In our opinion, these results help resolve the past difficulty in reconciling certain plesiomorphic features of *Ephedra* that are shared with the conifers, and must be considered homoplasious similarities when cycads are intracalated between the conifers and the gnetopsid–angiosperm clade.

Because of the great similarity of our results to those of Loconte & Stevenson (1990), it would be redundant to go into great detail on characters supporting the "ginkgophyte" clade. Likewise, the characters supporting the "anthophyte" clade (gnetopsids, angiosperms, and Bennettitales) have been discussed in great detail by Crane (1985), Doyle & Donoghue (1986a, b, 1987, 1992), and Donoghue (1989). We therefore concentrate here

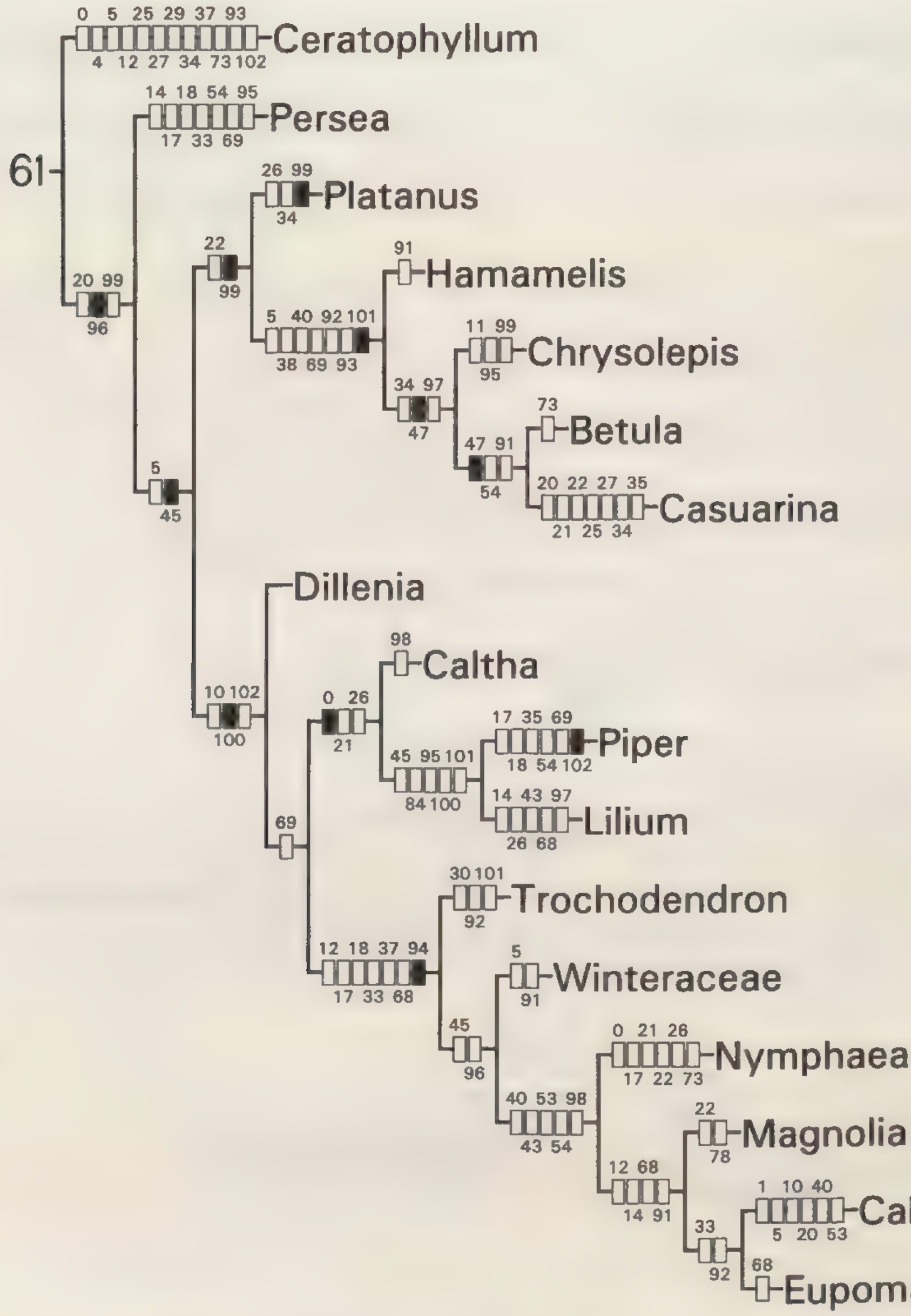

FIGURE 6. Upper section of tree in Figure 4, one of the most parsimonious trees found for matrix I (full data set). Hashmarks as in Figure 4.

on some of the novel clades found in our analyses as well as different character interpretations, which are outlined in Appendix A.

It is clear from comparison of our results with those of Loconte & Stevenson (1990) and Doyle & Donoghue (1986a, b, 1987, 1992) that the inclusion of fossils in the analysis can have a dramatic effect on the major structure of the tree. In particular, based on some manipulations of our data, it appears that certain features of the bennettitalean taxa support association of the "anthophytes" (gnetopsids and angiosperms) more closely with cycadalean features than with *Ginkgo* or the conifers; in our complete analyses, this resulted in *Ginkgo* placed basally on the conifer clade in some of the most parsimonious trees. When fossils are removed, these results are not found, and *Ginkgo* is consistently a sister taxon to the remainder of extant ginkgophytes. Because of the uncertainty in coding numerous characters of the fossil taxa, and, in particular, many of the reproductive and embryological features that most strongly support monophyly of gnetopsids and angiosperms, we view the results of the analyses including fossils as far more tentative than those using extant taxa alone.

In all of our analyses that included fossil taxa, the angiosperms, Bennettitales, and gnetopsids formed a monophyletic group in relation to the remainder of the seed plants. This supports the "anthophyte" clade of previous authors, with the exception that the position of *Pentoxylon* is variable depending on the analysis, and is either placed

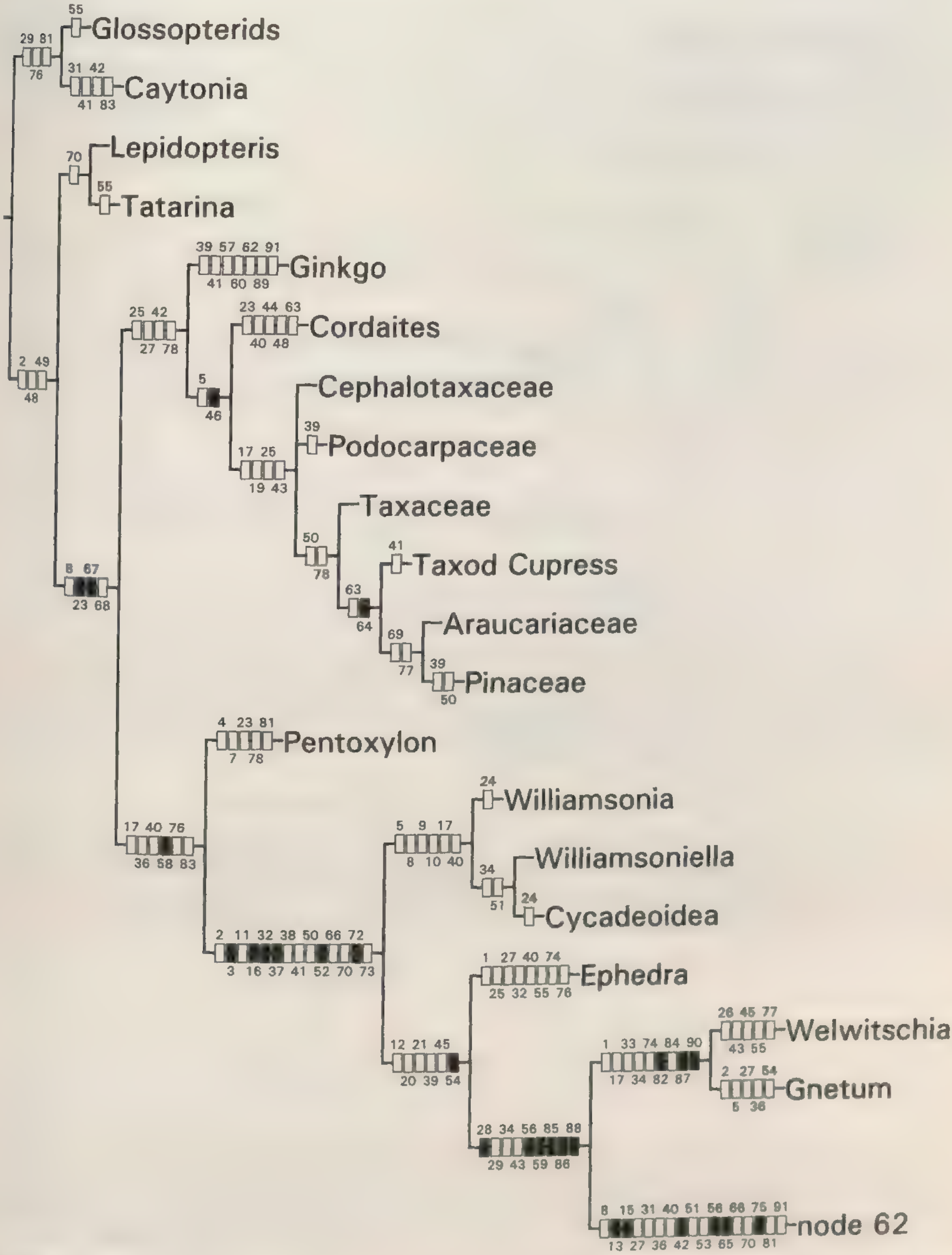

FIGURE 7. Middle section of another most parsimonious tree from analysis I (full data set). Hashmarks as in Figure 4.

as the sister taxon to the core group (Bennettitales–gnetopsids–angiosperms; Fig. 5), or in some cases, may be placed more distantly on the tree, outside of *Ginkgo* (Fig. 8), as reflected in the polytomy in Figure 3. This differs from the placement of *Pentoxylon* as a sister clade of the Bennettitales–gnetopsid group or solely the gnetopsid group in the analyses of Doyle & Donoghue (1986a, b, 1987, 1992) and its closer association with Bennettitales by Crane (1985). This difference is undoubtedly due in part to different codings of various characters, especially a different interpretation of the

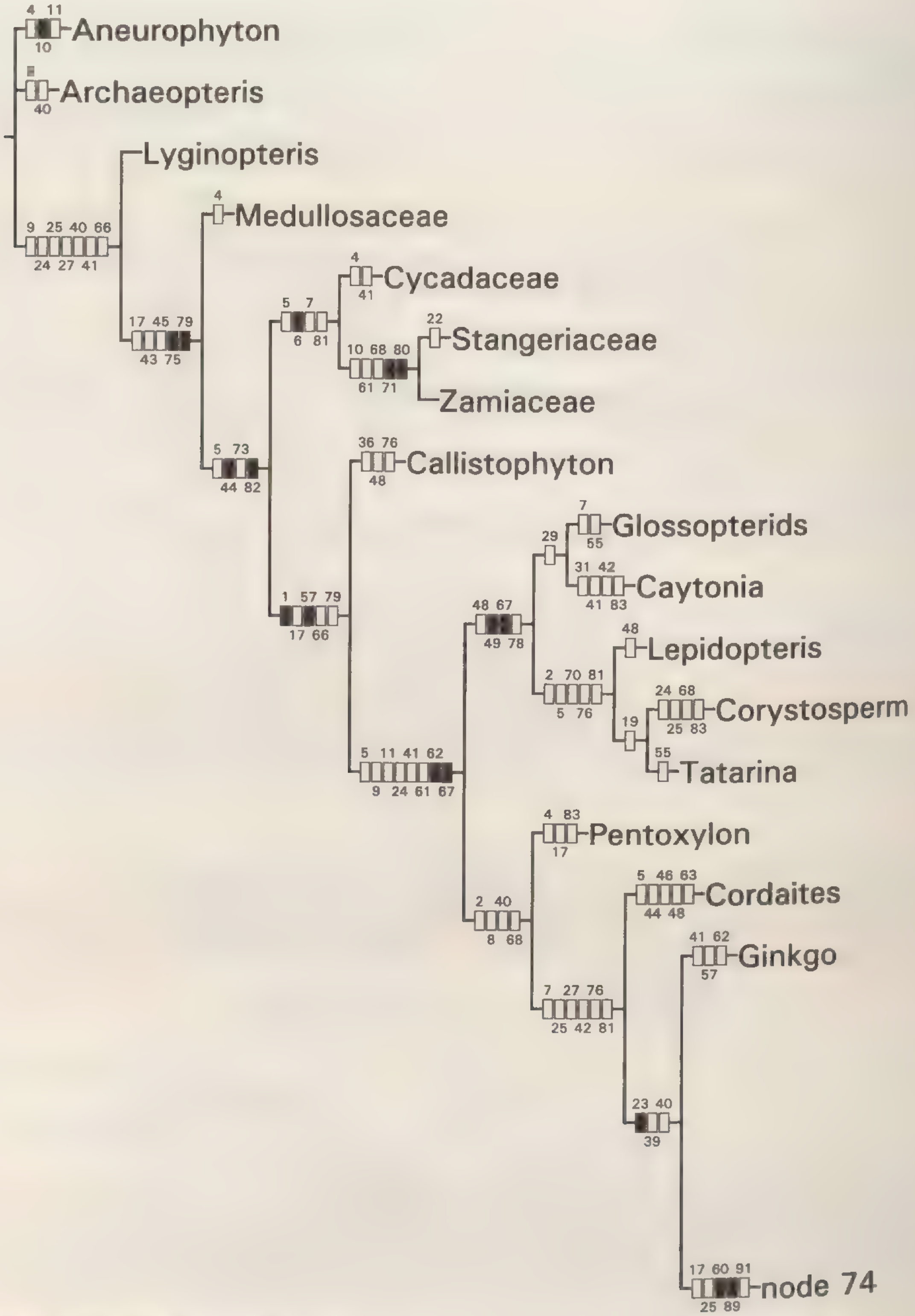

FIGURE 8. Basal portion of a third tree from analysis I (full data set). Hashmarks as in Figure 4.

cupulate structure of *Caytonia* as homologous with a second integument in *Pentoxylon* and the angiosperms. Our conclusion that the "second integument" of *Pentoxylon* has not been conclusively demonstrated resulted in coding of *Pentoxylon* as uncertain for the presence of an outer "seed envelope."

In all of our analyses, the gnetopsids (*Gnetum*, *Welwitschia*, *Ephedra*) were paraphyletic in all of the most parsimonious cladograms. However, it should be noted that trees with a monophyletic gnetopsid clade are only two steps longer than our most parsimonious trees in our complete analysis. When fossils were excluded and angiosperms con-

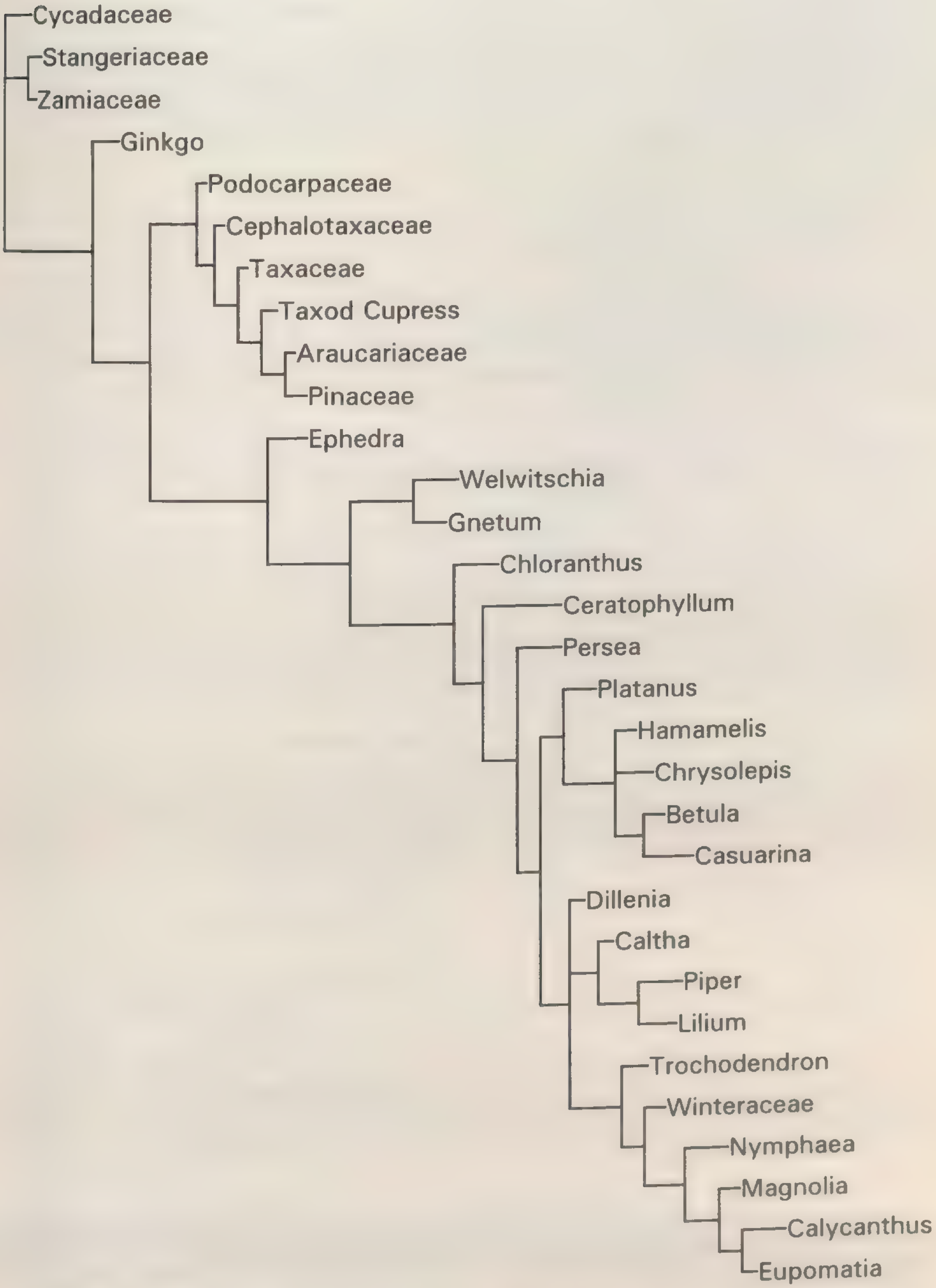

FIGURE 9. Strict consensus of trees found in analysis II (fossils excluded).

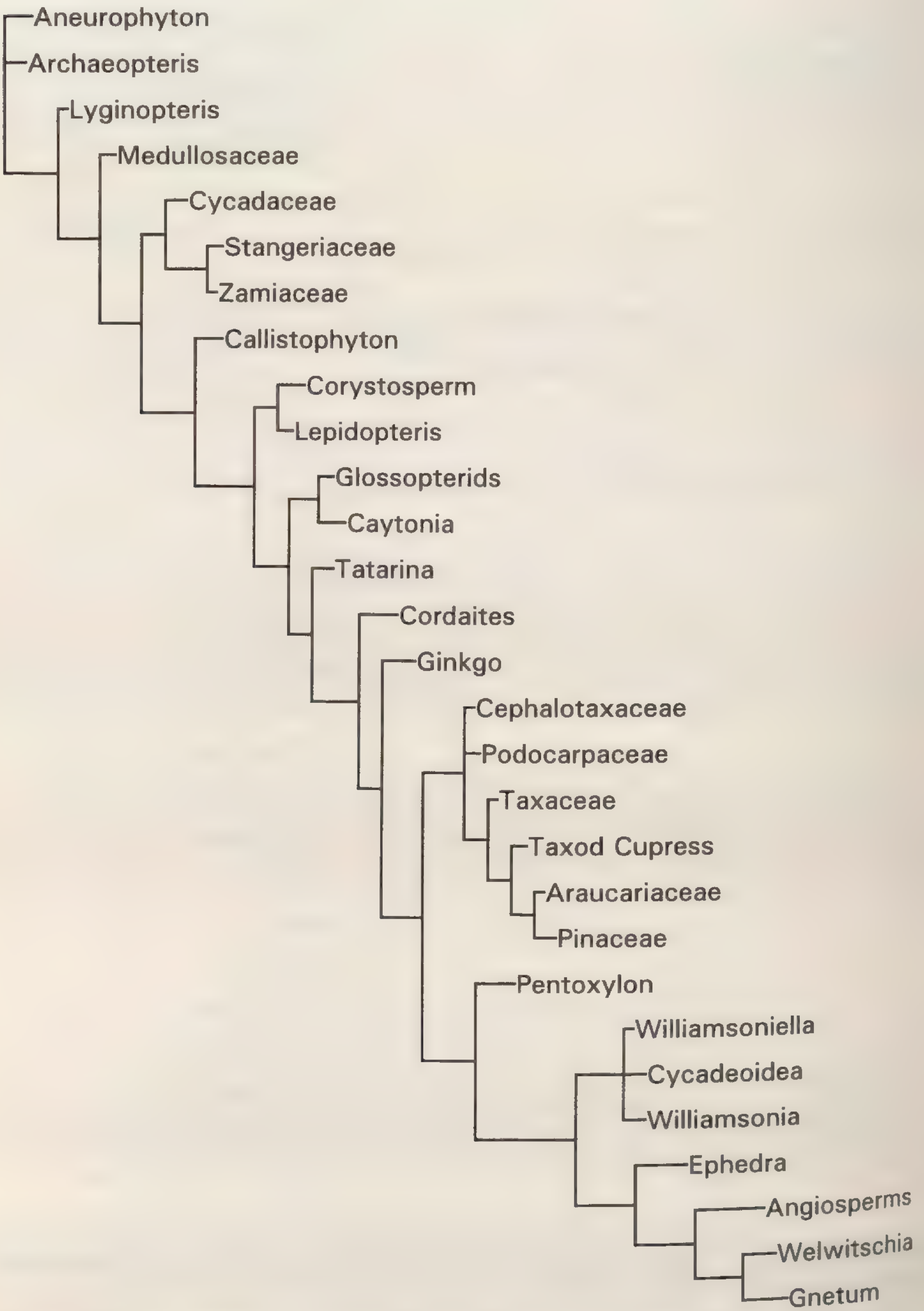

FIGURE 10. Strict consensus of trees found for matrix III (angiosperms condensed to single terminal).

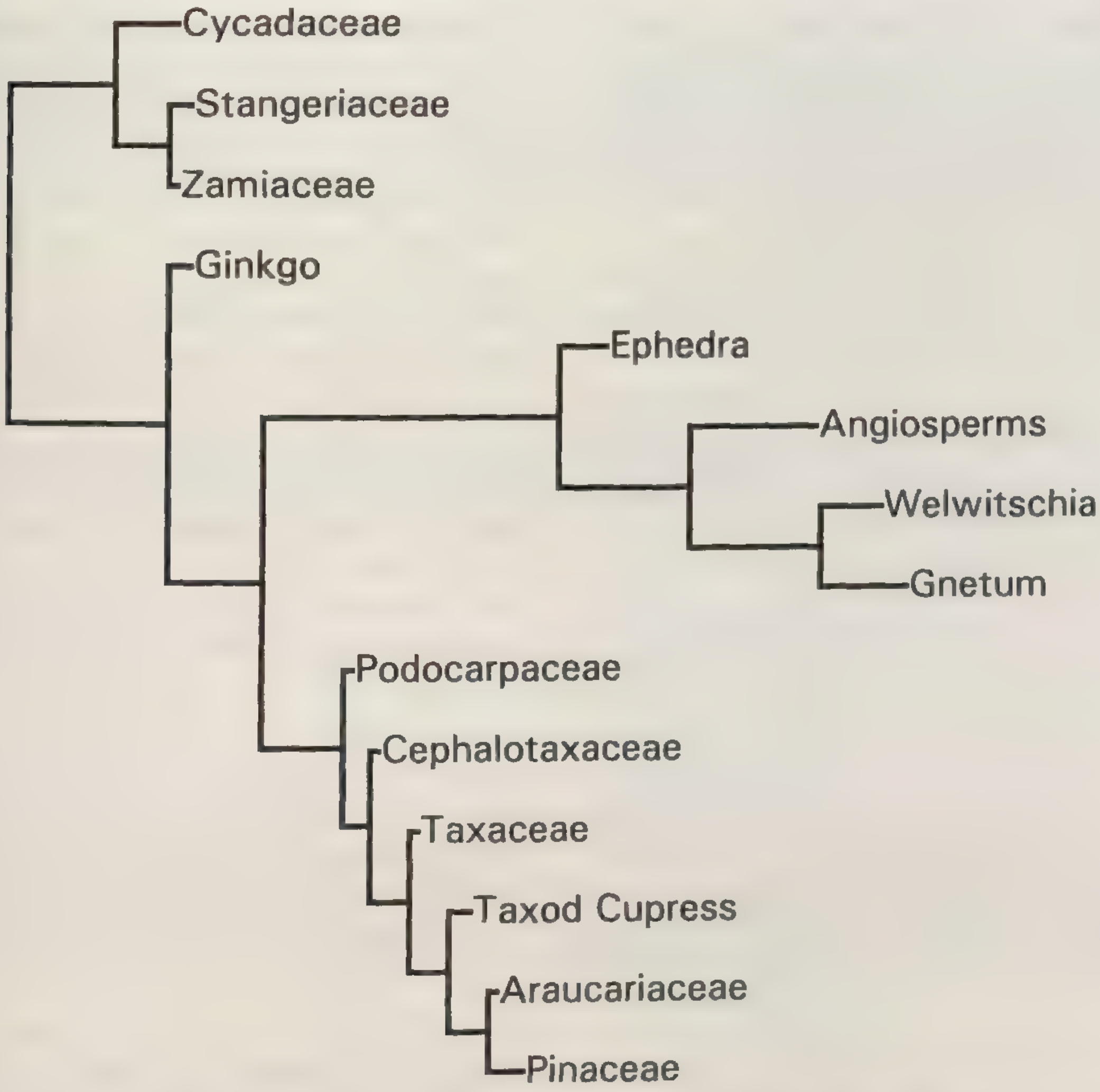

FIGURE 11. Single most parsimonious tree found for matrix IV (fossil tata excluded, angiosperms condensed).

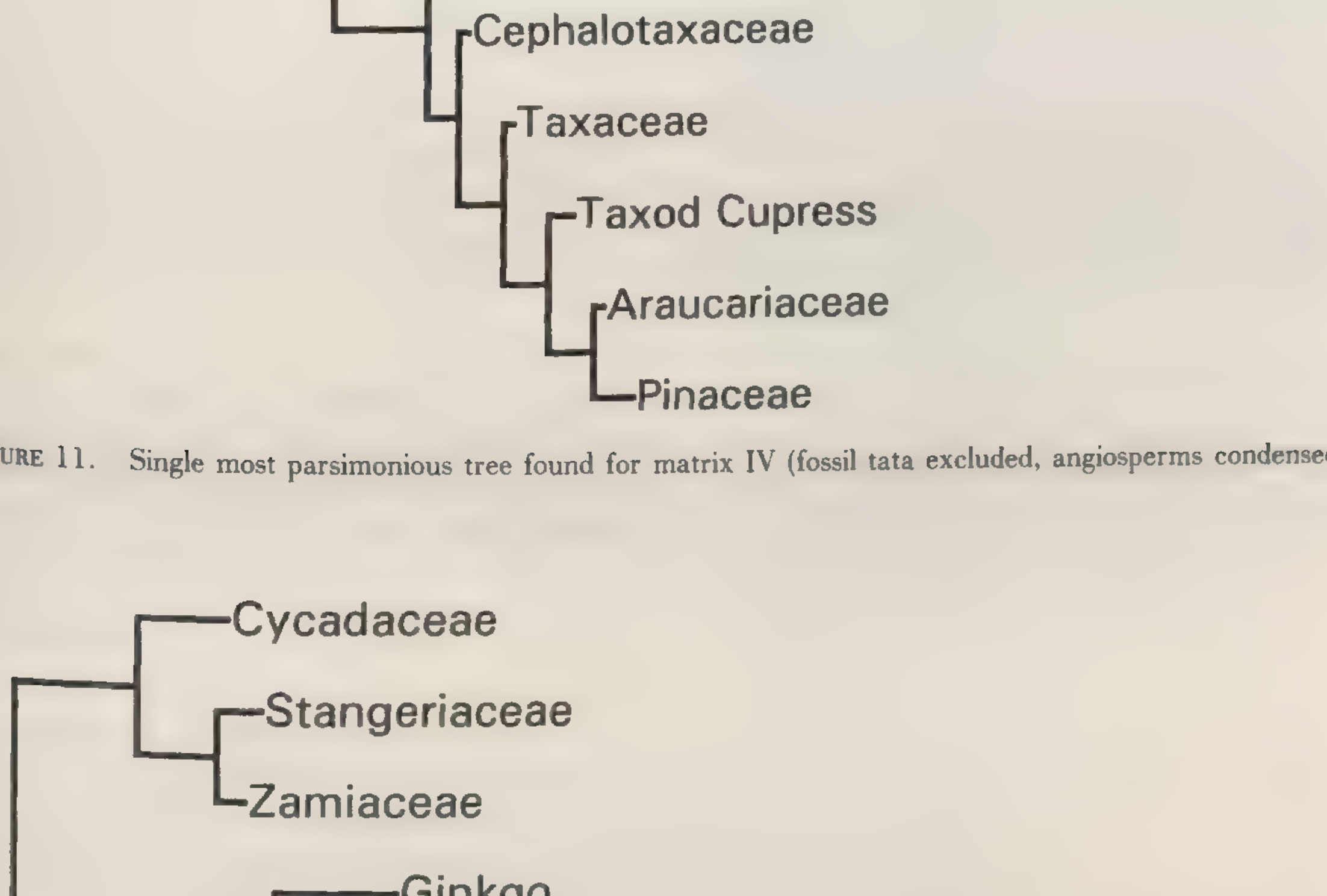

FIGURE 12. Strict consensus of trees found for matrix V (angiosperms and conifers condensed, fossils excluded).

densed (analysis IV), trees with a monophyletic gnetopsid clade were four steps longer (114 steps vs. 110 steps). The characters that support grouping of *Gnetum* and *Welwitschia* with the angiosperms to the exclusion of *Ephedra* include reduction in the microgametophyte, absence of the stalk cell, non-bifid inner integument (bifid only in the earliest developmental stages in *Ephedra*), non-alveolar megagametophyte, absence of archegonia, and cellular early embryogeny. These characters are constant as far as is known in angiosperms; additional characters that vary within angiosperms and support the *Gnetum*–*Welwitschia*–angiosperm grouping include the presence of a tetrasporic megagametophyte.

In all of the complete analyses of Doyle & Donoghue (1986a, b, 1987, 1992), the gnetopsids have been found to be monophyletic, associated with a monophyletic Bennettitales. Donoghue & Doyle (1989), in summarizing previous results, listed "unifying features" of the three gnetopsid genera as: "opposite leaves, circular bordered pits in the vessels, simple microsporophylls, one terminal ovule, and compound strobili." All of these features are either found in one or more angiosperm taxon (sometimes in combination), conifers, or can only realistically be coded as ambiguous in gnetopsids, angiosperms, or both (e.g., whether the angiosperm flower is interpreted as a compound or simple strobilus depends on interpretations of homology of the carpel, and conifers are generally interpreted as having compound megastrobili). We differ from Doyle and Donoghue in our interpretation of the nature of microsporophylls in *Ephedra* and *Welwitschia*, which seem to be clearly compound in both, but simple in *Gnetum* (see Appendix A). The "terminal ovule" of Gnetales, likewise, requires a specific interpretation in order to be scored as *not* homologous with certain angiosperms that have solitary, "terminal" ovules (e.g., Chloranthaceae, Piperaceae, Laurales, Platanaceae, Ceratophyllaceae, to name a few). Such characters are synapomorphies of the gnetopsid clade only when the primitive angiosperm archetype is assumed to lack them, an assumption not supported by observation of a broad array of taxa. Thus, by assuming a particular phylogenetic hypothesis for the angiosperms and extrapolating a primitive type (multiple ovules, foliar carpels = simple strobili, alternate leaves, spirally arranged simple microsporophylls), the character interpretations and coding of Doyle & Donoghue (1986a, b, 1987, 1992) and Donoghue & Doyle (1989) bias strongly against recognizing homologies between gnetopsids and angiosperms, and simultaneously bias their analyses in favor of an isolated, monophyletic Gnetales. This in turn has affected character optimization of the single angiosperm node in their analyses, which was then used as the basis for rooting later analyses within angiosperms (Donoghue & Doyle, 1989; Donoghue, 1989).

Based on our results, and the conflict of these results with those of previous studies (including Loconte & Stevenson, 1990), the question of whether the gnetopsids form a monophyletic group or are paraphyletic relative to the angiosperms (or to the angiosperms plus Bennettitales) remains a question that deserves much more attention. Since the evidence supporting their monophyly in previous morphological analyses was biased by assumptions about the nature of the primitive angiosperm, we feel that the answer to this problem can only be resolved by more careful analyses that include broader samples of angiosperm diversity and additional characters that can be scored unambiguously for gnetopsids and angiosperms. While our study has not resolved this issue, due to the limited sample of angiosperms that we included, the question of gnetopsid monophyly or paraphyly is now reopened.

The question of whether the seed plants are monophyletic was not directly addressed in our analyses, because we only included two terminals (*Aneurophyton*, *Archaeopteris*) that are considered to lack seeds. While the possibility of discovering a diphyletic origin of seed plants existed in our data set, it would require an *Aneurophyton* clade and an *Archaeopteris* clade of seed plants. This question should be addressed with a much larger sampling of both fossil and extant plants that lack seeds. Thus, we feel that the monophyly of seed plants in our results is not a significant conclusion from a cladistic standpoint. However, our "new" character of the bicornute or bifid apex of the seed, which was not used in previous cladistic analyses, is distributed in such a manner that it may provide more information than the "platyspermy-radiospermy" character that is commonly used in argumentation about seed origins. Thus, the cycad–lyginopterid–medullosan nonbifid form of seed might be found to be independently derived from the remainder of seed plants when more data are included. Undoubtedly, other ovule/seed characters can be developed which may help to shed light on this problem.

The proximity of the medullosans and cycads in our results is in contrast to the position of cycads and medullosans in Doyle & Donoghue (1986a, b, 1987, 1992). Our results are consistent with traditional hypotheses of the placement of medullosans

and cycads (e.g., Stewart & Delevoryas, 1956; Stewart & Rothwell, 1993; Taylor & Taylor, 1993) and more similar to the cladistic results of Crane (1985); they suggest that cycads may have originated from an ancestor that resembled medullosans in several respects. We find it difficult to envision the alternative (Doyle & Donoghue, 1986a, b, 1987, 1992; Donoghue, 1989) that the cycads are distant from the medullosans and form a monophyletic group with "anthophytes" excluding the conifers and *Ginkgo*.

Initially, we included four Mesozoic seed fern terminals in our analyses ("peltasperms," "corystosperms," "glossopterids," and "caytonia"), defined in essentially the same manner as Doyle & Donoghue (1986a, b, 1987). In many of those preliminary analyses the four Mesozoic seed fern terminals formed a monophyletic group near the Cordaites–conifer clade (Crepet et al., 1993). In our final analyses, however, we more carefully defined the terminals to be specific reconstructions (*Caytonia*, *Peltaspermum*, *Corystospermum*), as opposed to summaries of groups, and added *Tatarina* (considered to be a "peltasperm"). Of necessity, the glossopterid terminal remained a summary of several glossopterid taxa; we hope that in future analyses this can be remedied. In the analyses reported here, the five Mesozoic seed fern terminals do not consistently form a monophyletic group (e.g., Figs. 3, 4, 7), although they do form a monophyletic group, outside of *Ginkgo*, in some of the most parsimonious trees of our complete analysis. In our complete analysis, the peltasperms and corystosperm terminals move about in the various topologies, sometimes in positions "below" the *Ginkgo* clade and sometimes above the conifer clade, subtending the *Pentoxylon*–"anthophyte" clade. Likewise, *Pentoxylon* is found subtending the anthophyte clade in some trees (e.g., Fig. 5) but is associated with the pteridosperms, outside the *Ginkgo*–conifer–anthophyte clade, in others (Fig. 8).

Glossopterids and *Caytonia* formed a monophyletic group, outside of the ginkgophytes, in some of the most parsimonious trees in our complete analysis (e.g., Figs. 4, 8) and in all of the most parsimonious trees in the analysis that condensed angiosperms to a single terminal (III). This position "below" the *Ginkgo*–conifer–anthophyte clade in all most parsimonious trees in all relevant analyses contrasts sharply with the association of *Caytonia* with the "anthophyte" clade in some previous analyses (Doyle & Donoghue, 1986a, b, 1987, 1992). We interpret these differences to be due to different interpretations of structures (e.g., the "cupule" = second integument interpretation of Doyle & Donoghue, 1986a, b, 1987, 1992), the addition of new data both from the literature and from reinvestigations (e.g., the axial nature of the reproductive structures of *Corystosperms*, glossopterids, and *Caytonia* that were interpreted as sporophylls in previous analyses), and our restriction of some pteridosperm terminals (e.g., *Lepidopteris*) to represent specific reconstructions, as opposed to synthetic "composite" taxa.

In the context of a possible relationship between glossopterids and *Caytonia*, it is interesting to note that *Glossopteris*-like foliage (*Mexiglossa*) is known from the Middle Jurassic of Oaxaca, Mexico, in association with branched axes bearing sporangia that resemble *Caytonanthus* (Delevoryas & Gould, 1971; Delevoryas, 1969; Delevoryas & Person, 1975; Taylor & Taylor, 1993). In combination with our results, this suggests the possibility that the Northern Hemisphere *Caytonia* lineage is derived from an ancestor that is an offshoot of the earlier and highly diverse Gondwana glossopterids (which, of course, may not be monophyletic). Phylogenetic analyses of the Permian–Mesozoic seed ferns, and in particular the glossopterids, in which careful reconstructions of individual taxa are undertaken as opposed to treating them as synthetic groups, is long overdue.

We find the traditional placement of *Cordaites* with the conifer clade in some, but not all, of our fossil analyses. In trees with *Ginkgo* on the conifer clade, *Cordaites* is the "next" branch, as often found in previous analyses (Crane, 1985; Doyle & Donoghue, 1986a, b, 1987, 1992). In contrast, the placement of *Ginkgo* outside the conifer–anthophyte clade is consistent with the notion that it shares numerous plesiomorphic features with Mesozoic seed ferns, but shares few if any synapomorphies that would place it with conifers at the exclusion of the Mesozoic seed ferns. We concur with Qin-er (1993) that the female reproductive structure of *Ginkgo* can be interpreted as an axillary seed-bearing structure subtended by a leaf, these borne on a seasonally determinate structure that may be homologous to the determinate compound cone axis of conifers (but not as densely aggregated nor completely determinate). Thus, the determinate compound strobilus becomes a synapomorphy of the conifer–anthophyte group; and, under such an interpretation, the carpel of angiosperms would be derived from a seed-bearing axis (simple cone = placenta) subtended by a leaf. Such a structure would be homologous to the bract-ovuliferous scale complex of conifers, the leaf-seed-bearing-axis of *Ginkgo*, and possibly to the leaf-

seed-bearing-axis in glossopterids. Such a homology would be general, suggesting that the subtending leaf of glossopterids, and possibly the "cupule" of *Caytonia* are homologous appendages to the "leaf" portion of the angiosperm carpel; but, relative to conifers and *Ginkgo*, this homology would be simply a shared plesiomorphy of *Caytonia* and *angiosperms*, with independent infolding of the bract to envelop the seeds in the two groups. Our results suggest such possible broad homologies of strobilus organization, but also, because of the position of *Caytonia* and glossopterids, argue that carpels in angiosperms are homologous with the cupule/seed complex of *Caytonia* at the same level as the bract-ovuliferous scale complex of conifers.

It is interesting to note that the results obtained here for relationships within conifers are considerably different from those obtained by either Hart (1987) or Miller (1988). Most notable is the placement of Podocarpaceae and/or Cephalotaxaceae as the first branch of the conifer clade in our analyses, in contrast to the basal position of Taxaceae (Miller, 1988) or Pinaceae (Hart, 1987) in other analyses. On the other hand, it is interesting that the Podocarpaceae, Cephalotaxaceae, and Taxaceae are the first three branches, respectively, in our results. Historically, systematists have suggested in one way or another relationships between these three families, but without synapomorphies to unite them. A plesiomorphic assemblage perhaps best expresses this situation.

The position of *Callistophyton* in all of our analyses that include fossils was consistently below the "ginkgophyte" clade, including the Permian–Mesozoic seed ferns, and "above" the cycads, lyginopterids, and medullosans. We did not find a close association of *Callistophyton* with the conifer clade, as has been proposed by some authors (e.g., Rothwell, 1982). However, some characters shared by Mesozoic seed ferns and at least some conifers may represent shared plesiomorphies retained from a callistophytalean-like ancestor; this is consistent with numerous of the trees found in our complete analysis.

The intent of our analyses has not been to evaluate patterns within angiosperms, and our sample is insufficient to make any firm conclusions about phylogeny within the angiosperm clade. Whether or not our sample within angiosperms has been sufficient to stabilize the placement of angiosperms relative to other seed plants remains to be seen, as discussed below. We consider our results to be more an indication of the preliminary nature of all seed plant/angiosperm analyses up to this point, and expect numerous differences from our results within angiosperms in future analyses. Certainly, additional characters need to be included to provide greater resolution within angiosperms, which may also affect the relationships of the angiosperm clade to outgroups and outgroups to each other.

Over the past century, much emphasis has been placed on the question of which modern angiosperms most closely resemble the "ancestral" angiosperm (e.g., Arber & Parkin, 1907; Cronquist, 1981). In more recent cladistic studies, emphasis has been placed on determining the "first branch" of the angiosperms. While such questions have immediate appeal, it should be pointed out that: (1) the first, or "ancestral," member of any monophyletic group did not necessarily resemble the extant lineage of the "first branch" (sister clade of the remainder of the group), because of autapomorphic features developed since the time of divergence; (2) the concept of "first branch" is itself confounded, since the sister group of the "first branch" is equally the "first branch." It is probably preferable to refer to such "first" or "basal" branches as "one of the basal branches" or "most plesiomorphic terminal" but unfortunately, such terminology is unwieldy.

If the gnetopsid group is paraphyletic relative to the angiosperms, then our best estimate of the primitive angiosperm will still be affected by parsimony analysis within angiosperms. Unfortunately, the popular notion that we can estimate the ancestral state of a group by inference, if we know the topology of outgroup taxa, is erroneous (Nixon & Carpenter, in press) and has been based at least in part on misinterpretation of Maddison et al. (1984). Likewise, the ingroup topology of the angiosperm clade, and which angiosperm taxa are sampled, will affect the topology of outgroups; thus, we hope that methods of compartmentalization (e.g., Maddison et al., 1984) will be replaced by broader sampling within groups and simultaneous analysis of ingroup and outgroup pattern. How to determine when samples are of sufficient breadth to produce reliable and stable results is still an area of active research.

Using DADA, constrained analyses were input to Hennig86; with DADA, taxa can be constrained to be grouped into certain topologies, but taxa may also be allowed to "float" by assigning ambiguous group membership variables. When the cycads were constrained to form a monophyletic group with gnetopsids and angiosperms, but allowing the pteridosperms to "float" (not constrained, either inside or outside of the group), for the complete data set, the tree was two steps longer. When the topology was constrained to the results of Doyle & Donoghue

(e.g., 1992) for cycads and anthophytes (monophyletic gnetopsids, *Pentoxylon* part of gnetopsid clade, these two a sister group to a monophyletic Bennettitales), the trees are at least 16 steps longer. If the pteridosperms are allowed to "float" in such trees, surprisingly, they are a basal part of the *Ginkgo*–conifer clade in all most parsimonious trees; if they are constrained within the cycad–anthophyte assemblage, the trees are even longer than 16 steps, depending on the extent to which the analysis is constrained. Successive weighting of the complete matrix (Hennig86, xsteps w command) results in two trees; *Ginkgo* is placed outside of the conifer–anthophyte group in both these trees. The trees differ only in placement of Cephalotaxaceae and Podocarpaceae as alternative basal branches within the conifer clade. The trees are similar to those found in analysis IV (angiosperms condensed to a single terminal), with *Pentoxylon* subtending the anthophyte clade, and glossopterids and *Caytonia* forming a monophyletic group below the "ginkgophyte" clade.

THEORETICAL ASPECTS

The results of various manipulations of our data matrix, by excluding or including fossil taxa, and fusing multiple taxa into single terminals, have several broader implications for these types of analyses. It is clear that sample size and distribution of taxa are extremely important. Compartmentalization (by treating diverse taxa as single polymorphic terminals) may result in very different results, even if the compartmentalized group is monophyletic in all uncompartmentalized analyses (e.g., the angiosperms in our analyses). These phenomena are independent of what the "correct" phylogeny may be; the fact that such changes in results occur is of interest outside of whether one or the other solution is "more" correct. When the angiosperms are treated as a single polymorphic terminal, allowing *more* possible combinations to be basal within the angiosperms, fewer topologies are found outside of the angiosperms (e.g., *Pentoxylon* always basal to the anthophyte clade, in contrast to the unresolved position of *Pentoxylon*) than when the component angiosperm taxa are sampled. While this might seem counterintuitive, it is consistent with the effects of ambiguity and polymorphism reported by Nixon & Davis (1991). Thus, scoring a taxon as polymorphic does not necessarily allow more possibilities for its relationship to other taxa, and likewise does not result in predictable loss of overall resolution. The internal combinations of polymorphisms themselves either restrict or expand the possibilities for both ingroup and outgroup topologies, in ways that appear to be tractable only through observation of ingroup variation and breaking up of ingroup taxa into monothetic units.

UNDERSAMPLING

Undersampling of any pattern that is not perfectly hierarchic will in general result in increased levels of hierarchy in the data, potentially resulting in false hierarchy (see Nixon & Wheeler, 1991). Homoplasy in cladograms (error, e.g., the inability to distinguish homology from nonhomology) results in deviation from perfect hierarchic structure; the greater the level of homoplasy, the greater the problem of false hierarchy associated with undersampling. In broad analyses of the type undertaken here, homoplasy may be due to an inability to distinguish parallel or otherwise independent origins of structures, or inability to see that two structures are actually homologous; in all cases, homoplasy should not be considered something that occurs in nature, but instead is simply error in the interpretation of characters (the concepts of parallelism and convergence refer to evolutionary *interpretations* of homoplasy). Of necessity, our analyses, like other previous analyses, suffer from this problem, particularly in our limited sample of angiosperm taxa. Unfortunately, within angiosperms, we feel that it is not possible at this time to summarize character distributions for large groups of taxa, since at this point there is very little consensus among the results of phylogenetic analyses, most of which suffer from the very problems that we have discussed here. Thus, we anticipate that as additional angiosperm taxa are added, patterns may change and eventually stabilize on particular patterns, both within and outside of the angiosperms, when samples become sufficient. It is impossible at this point to predict what adequate sample sizes may be.

MISSING DATA

There can be little doubt that missing data introduce uncertainty into cladistic analysis, but to date there is no method to measure such uncertainty, nor to predict its effects. A widely held belief (from our experience with students and colleagues), is that missing data will merely increase the number of equally parsimonious solutions but that the solution will still include the shortest trees that would be found if missing data were known. This is definitely not the case (Nixon, in prep.; see also Nixon & Davis, 1991), and is related to the problem of

undersampling and homoplasy discussed above. Thus, if there is no homoplasy in the data, substituting missing data for real data will only result in less resolved trees, the strict consensus of which will not be in conflict with the original trees based on full data sets. However, with greater levels of homoplasy, increasing levels of missing data increase the likelihood that some or *all* trees found may be in conflict with the original trees. In extreme examples, the original trees may not be found at all. This can be extrapolated from the examples for polymorphism (ambiguity) illustrated by Nixon & Davis (1991). Specific patterns within groups (restricting the states for basal groups), when considered ambiguous, may actually *restrict* the equally parsimonious solutions, by allowing the terminal to join another clade that reduces homoplasy in other characters that have been scored properly. The problem of homoplasy interacting with missing data is thus severe, and we have not escaped it in our analyses, which have levels of missing data varying from 8 to 24% and consistency indices in the range of 0.39–0.79. The other aspect of this problem which has not been explored is the nature of ambiguity in the data; for instance, we scored several characters that are known only within angiosperms (e.g., floral characters) as nonapplicable (represented by a dash in Table 1) for non-angiosperms. Because the angiosperms are monophyletic in all analyses, such missing data will not have the kinds of effects outside the angiosperms that dispersed missing values will have when they actually contribute to placement of taxa. This area needs further investigation, and perhaps characters scored as inapplicable when all applicable scores form a monophyletic group should be reported separately from other kinds of ambiguity in the data.

Conclusions

Our analyses support the Loconte & Stevenson (1990) results in terms of the phylogenetic relationships of extant seed plants as (cycads (ginkgo conifers (gnetopsid–angiosperms))). This pattern is immutable throughout the various manipulations of our data. Thus, we reject the closer connection of cycads with the gnetopsid–angiosperm clade found in the studies of Doyle & Donoghue (1986a, b, 1987, 1992).

While our analyses are not definitive in regard to relationships of angiosperms to gnetopsids and Bennettitales, it is apparent that a closer relationship of angiosperms with the extant gnetopsids than has been proposed in recent studies must be considered, and the possibility that the "gnetopsid" group is paraphyletic bears close attention. Because of the major role that morphological analyses must play in any total evidence analysis, and because fossil data are largely restricted to morphology, our eventual understanding of the origin of angiosperms must be based on further, detailed comparative work among gnetopsids (and other seed plants) and a broad sample of angiosperms. Compartmentalized studies, at this point in time, will fail because the most parsimonious placement of any diverse group can only be determined by simultaneously including evidence of the structure of internal variation within the group. Compartmentalization has been applied directly by Donoghue & Doyle (1989) in their within-angiosperm analyses, which were based in part on previous results of seed plant analyses. Subsequently, Donoghue (1989) joined three separately produced cladograms for seed plants (Doyle & Donoghue, 1986b), basal angiosperms (Donoghue & Doyle, 1989), and conifers (Hart, 1987), and mapped characters such as "dioecy" onto the composite cladogram. These kinds of studies relax global parsimony, so that the "composite" cladograms are not guaranteed, nor, in our opinion, even likely, to be the most parsimonious topologies for the characters that are mapped. Additionally, the analysis by Donoghue (1989), built upon a previous analysis that had at least some unjustifiable character codings for the compartmentalized angiosperm taxon (e.g., alternate phyllotaxy, spiral microsporophylls, and others discussed above), and questionable codings for some taxa (e.g., "angiosperms") of the character (dioecy) under investigation. At present, when conflicting results are commonplace among and between data sets from a wide array of data sources, it seems premature to attempt to draw anything but very broad conclusions from these data. Any rush to map evolutionary scenarios onto existing cladograms seems rather futile.

Within angiosperms, *Chloranthus* and *Ceratophyllum* were the "first branches" in various of our analyses. In constrained analyses, a monophyletic gnetopsid group favors *Ceratophyllum* as a basal branch of the angiosperms (and vice versa), while *Chloranthus* as a basal branch favors a paraphyletic gnetopsid group (and vice versa). This, as well as numerous other examples in our data, illustrates the interdependency of subtree topology under the criterion of global parsimony. Such interdependency of clades may call into question not only compartmentalization but also clade support

statistics (e.g., the bootstrap or Bremer (1988) support; see also Donoghue et al., 1992), which attempt to measure reliability or confidence in particular branches of cladograms, in isolation from other branches. Individual branches within cladograms clearly are not independent events relative to the occurrence of other branches; trees occur as wholes, not isolated clades, and changes within one clade may have dramatic effects in other parts of the tree. With morphological data, new methods that are in development (Davis et al., 1993; Davis, 1993) may offer more useful ways of measuring quality of trees, as well as stability of clades; successive character removal, for example, identifies particular characters that are necessary for the support of particular groups, even when these characters do not change on the branch under consideration.

Finally, we urge readers to view our results only as a preliminary basis for examining a range of hypotheses about seed plant relationships. This range of hypotheses is somewhat broader than previous hypotheses for certain groups, we feel, because we have tied our data more directly to observed characters, as opposed to theoretically constructed terminals, for cycads, conifers, and angiosperms. Currently, most data on both fossil and extant seed plants are fragmentary, based on small samples, with low reliability and comparability across studies. The most important advances in our understanding of seed plant and angiosperm phylogeny will be made by careful comparative morphological and molecular studies that take into consideration the issues of sampling, taxon definition, and character coding that have such dramatic influence on the outcome of any cladistic analysis.

Literature Cited

Albert, V. A., A. Backlund, K. Bremer, M. W. Chase, J. R. Manhart, B. D. Mishler & K. C. Nixon. 1994. Functional constraints and *rbc*L evidence for land plant phylogeny. Ann. Missouri Bot. Gard. 81: 534–567.

Anderson, J. M. & H. M. Anderson. 1983. Palaeoflora of South Africa, Molteno Formation (Triassic), Vol. 1 (Part 1). Introduction, Part 2. *Dicroidium*. A. A. Balkema, Rotterdam.

Antevs, E. 1914. *Lepidopteris Ottonis* (Gopp.) Schimp. and *Antholithus Zeilleri* Nath. Kungl. Svenska Vetenskapsakad. Handl. 51(7): 1–18.

Arber, E. A. N. & J. Parkin. 1907. On the origin of angiosperms. J. Linn. Soc. Bot. 22: 29–80.

Archangelsky, S. 1968. Studies on Triassic fossil plants from Argentina. IV. The leaf genus *Dicroidium* and its possible relation to *Rhexoxylon* stems. Palaeontology 11: 500–512.

——— & D. W. Brett. 1961. Studies on Triassic fossil plants from Argentina. I. *Rhexoxylon* from the Ischgualasto Formation. Philos. Trans., Ser. B 244: 1–19.

Arnold, C. A. 1935. On seedlike structures associated with *Archaeopteris*, from the Upper Devonian of Northern Pennsylvania. Contr. Mus. Paleontol. Univ. Michigan 4: 283–286.

Baxter, R. W. 1949. Some pteridospermous stems and fructifications with particular reference to the Medullosaceae. Ann. Missouri Bot. Gard. 36: 287–352.

Beck, C. B. 1960. Connection between *Archaeopteris* and *Callixylon*. Science 131: 1524–1525.

———. 1971. On the anatomy and morphology of lateral branch systems of *Archaeopteris*. Amer. J. Bot. 58: 758–784.

———, R. Schmidt & G. W. Rothwell. 1982. Stelar morphology of the primary vascular system of seed plants. Bot. Rev. 48: 691–815.

Behnke, H. D. 1988. Sieve element plastids, phloem protein, and evolution of flowering plants. III. Magnoliidae. Taxon 37: 699–732.

Bessey, C. E. 1897. Phylogeny and taxonomy of the angiosperms. Bot. Gaz. (Crawfordsville) 24: 154–178.

Bierhorst, D. 1971. Morphology of Vascular Plants. Macmillan, New York.

Boke, N. 1976. Dichotomous branching in *Mamillaria* (Cactaceae). Amer. J. Bot. 63: 1380–1384.

Bonamo, P. M. 1977. *Rellimia thomsonii* (Progymnospermopsida) from the Middle Devonian of New York State. Amer. J. Bot. 64: 1272–1285.

———. 1983. *Rellimia thompsonii* (Dawson) Leclercq and Bonamo (1973): The only correct name for the aneurophytalean progymnosperm. Taxon 32: 449–454.

——— & H. P. Banks. 1967. *Tetraxylopteris schmidtii*: Its fertile parts and its relationships within the Aneurophytales. Amer. J. Bot. 54: 755 768.

Bose, M. N., P. K. Pal & T. M. Harris. 1985. The *Pentoxylon* plant. Philos. Trans., Ser. B 310: 77–108.

Bouman, F. 1984. The ovule. Pp. 123–157 *in* B. Johri (editor), Embryology of Angiosperms. Springer-Verlag, Berlin.

Bremer, K. 1988. The limits of amino-acid sequence data in angiosperm phylogenetic reconstruction. Evolution 42: 795–803.

Brown, H. P. & A. J. Panshin. 1934. Identification of the Commercial Timbers of the United States. McGraw-Hill, New York.

Buckland, W. 1827. Session of June 5, 1827. Proc. Geol. Soc. London 1: 80–81.

———. 1828. On the Cycadeoideae, a family of fossil plants found in the oolite quarries of the Isle of Portland. Trans. Geol. Soc. (London) 2: 395–401.

Burger, W. C. 1977. The piperales and the monocots: Alternative hypotheses for the origin of monocotyledonous flowers. Bot. Rev. 43: 345–393.

———. 1981. Heresy revived: The monocot theory of angiosperm origin. Evol. Theory 5: 189–225.

Carluccio, L. M., F. M. Hueber & H. P. Banks. 1966. *Archaeopteris macilenta*, anatomy and morphology of its frond. Amer. J. Bot. 53: 719–730.

CHAMBERLAIN, C. J. 1935. Gymnosperms, Structure and Evolution. Univ. Chicago Press, Chicago.

CLARK, C. & D. J. CURRAN. 1986. Outgroup analysis, homoplasy, and global parsimony: A response to Maddison, Donoghue, and Maddison. Syst. Zool. 35: 422–426.

CRANE, P. R. 1985. Seed plant phylogenetics. Ann. Missouri Bot. Gard. 72: 716–793.

———. 1986. The morphology and relationships of the Bennettitales. Pp. 163–175 *in* R. A. Spicer & B. A. Thomas (editors), Systematic and Taxonomic Approaches to Palaeobotany. Clarendon Press, Oxford.

———. 1988. Major clades and relationships in the "higher" gymnosperms. Pp. 218–272 *in* C. B. Beck (editor), Origin and Evolution of the Gymnosperms. Columbia Univ. Press, New York.

CREPET, W. L. 1972. Pollination mechanisms in *Cycadeoidea*. Amer. J. Bot. 59: 1048–1056.

———. 1974. Investigations of North American cycadeoids: The reproductive biology of *Cycadeoidea*. Palaeontographica, Abt. B., Paläophytol. 148: 144–169.

———, E. M. FRIIS & K. C. NIXON. 1991. Fossil evidence for the evolution of biotic pollination. Philos. Trans., Ser. B 333: 187–195.

———, K. C. NIXON, D. W. STEVENSON & E. M. FRIIS. 1993. The relationships of seed plants in reference to angiosperm outgroups. Amer. J. Bot. 80: 123. [Abstract.]

CRONQUIST, A. 1981. An Integrated System of Classification of Flowering Plants. Columbia Univ. Press, New York.

DAVIS, J. I. 1993. Character removal as a means for assessing stability of clades. Cladistics 9: 201–210.

———, M. W. FROHLICH & R. J. SORENG. 1993. Cladistic characters and cladogram stability. Syst. Bot. 18: 188–196.

DELEVORYAS, T. 1955. The Medullosae-structure and relationships. Palaeontographica, Abt. B., Paläophytol. 97: 114–167.

———. 1959. Investigations of North American cycadeoids: *Monanthesia*. Amer. J. Bot. 46: 657–666.

———. 1963. Investigations of North American cycadeoids: Cones of *Cycadeoidea*. Amer. J. Bot. 50: 45–52.

———. 1968. Investigations of North American cycadeoids: Structure, ontogeny, and phylogenetic considerations of cones of *Cycadeoidea*. Palaeontographica, Abt. B, Paläophytol. 121: 122–133.

———. 1969. Glossopterid leaves from the Middle Jurassic of Oaxaca, Mexico. Science 165: 895–896.

——— & R. E. GOULD. 1971. An unusual fossil fructification from the Jurassic of Oaxaca, Mexico. Amer. J. Bot. 58: 616–620.

——— & J. MORGAN. 1954. A new pteridosperm from Upper Pennsylvanian deposits of North America. Palaeontographica, Abt. B, Paläophytol. 96: 12–23.

——— & C. P. PERSON. 1975. *Mexiglossa varia* gen. et sp. nov. A new genus of glossopterid leaves from the Jurassic of Oaxaca, Mexico. Palaeontographica, Abt. B, Paläophytol. 154: 114–120.

DONOGHUE, M. J. 1989. Phylogenies and the analysis of evolutionary sequences, with examples from seed plants. Evolution 43: 1137–1156.

——— & J. A. DOYLE. 1989. Phylogenetic studies of seed plants and angiosperms based on morphological characters. Pp. 181–193 *in* B. Fernholm, K. Bremer & H. Jornvall (editors), The Hierarchy of Life. Elsevier Science, New York.

———, R. G. OLMSTEAD, J. F. SMITH & J. D. PALMER. 1992. Phylogenetic relationships of Dipsacales based on *rbc*L sequences. Ann. Missouri Bot. Gard. 79: 333–345.

DOYLE, J. A. & M. J. DONOGHUE. 1986a. Relationships of angiosperms and Gnetales: A numerical cladistic analysis. Pp. 177–198 *in* R. A. Spicer & B. A. Thomas (editors), Systematic and Taxonomic Approaches to Palaeobotany. Clarendon Press, Oxford.

——— & ———. 1986b. Seed plant phylogeny and the origin of the angiosperms: An experimental cladistic approach. Bot. Rev. 52: 321–431.

——— & ———. 1987. The origin of angiosperms: A cladistic approach. Pp. 17–50 *in* E. M. Friis, W. G. Chaloner & P. R. Crane (editors), The Origin of Angiosperms and the Biological Consequences. Cambridge Univ. Press, Cambridge.

——— & ———. 1992. Fossils and seed plant phylogeny reanalyzed. Brittonia 44: 89–106.

DUFEK, D. & B. M. STIDD. 1981. The vascular system of *Dolerotheca* and its phylogenetic significance. Amer. J. Bot. 63: 887–907.

DURANTE, M. V. 1992. Angaran upper permian flora of the Nan-Shan Section (Northern China). Sino-Swedish Exped., Publ. 55: 561–568.

EAMES, A. 1952. Relationships of the Ephedrales. Phytomorphology 2: 79–100.

———. 1961. Morphology of the Angiosperms. McGraw Hill, New York.

ECKENWALDER, J. 1976. Re-evaluation of Cupressaceae and Taxodiaceae: A proposed merger. Madroño 23: 237–256.

EGGERT, D. A. & T. DELEVORYAS. 1960. *Callistomarion*—A new seed genus from the Upper Pennsylvanian of Illinois. Phytomorphology 10: 323–360.

——— & G. W. ROTHWELL. 1979. *Stewartiotheca* gen. n. and the nature and origin of complex permineralized medullosan pollen organs. Amer. J. Bot. 66: 851–866.

FARRIS, J. S. 1972. Estimating phylogenetic trees from distance matrices. Amer. Naturalist 106: 645–668.

———. 1982. Outgroups and parsimony. Syst. Zool. 31: 328–334.

———. 1988. Hennig86. Program and Documentation. Published by the author, Port Jefferson, New York.

FEISTMANTEL, O. 1876. Versteinerungen der bohmischen Kohlenablagerungen. Palaeontographica, Abt. B, Paläeophytol. 23: 223–316.

FISHER, J. 1973. Axillary and dichotomous branching in the palm *Chamaedorea*. Amer. J. Bot. 60: 1046–1056.

———. 1976. Development of dichotomous branching and axillary buds in *Strelitzia* (Monocotyledonae). Canad. J. Bot. 54: 578–592.

FLORIN, R. 1936. On the structure of the pollen-grains in the Cordaitales. Svensk Bot. Tidskr. 30(3): 624–651.

———. 1950. On female reproductive organs in the Cordaitinae. Acta Horti Berg. 15(6): 111–134.

———. 1951. Evolution in cordaites and conifers. Acta Horti Berg. 15: 285–388.

FRIIS, E. M., P. R. CRANE & K. R. PEDERSEN. 1988.

Reproductive structure of Cretaceous Platanaceae. Biol. Skr. 31: 1–56.

GALTIER, J. 1988. Morphology and phylogenetic relationships of early pteridosperms. Pp. 135–176 *in* C. B. Beck (editor), Origin and Evolution of Gymnosperms. Columbia Univ. Press, New York.

——— & J. C. HOLMES. 1982. New observations on the branching of Carboniferous ferns and pteridosperms. Ann. Bot. 49: 737–746.

GAU, Z. & B. THOMAS. 1989. A review of fossil cycad megasporophylls, with new evidence of *Crossozamia* Pomel and its associated leaves from the Lower Permian of Taiyuan, China. Rev. Palaeobot. Palynol. 60: 204–223.

GAUSSEN, H. 1946. Les Gymnospermes, actuelles et fossiles. Trav. Lab. Forest. Toulouse, Tome 2, Etud. Dendrol., Sect. 1, 1(3,5): 1–26.

GIFFORD, E. M. & G. E. CORSON. 1971. The shoot apex in seed plants. Bot. Rev. 37: 143–229.

——— & A. FOSTER. 1988. Morphology and Evolution of Vascular Plants, 3rd ed. W. H. Freeman, New York.

GOLOBOFF, P. 1993. NONA. Program and documentation. Published by the author, New York, New York.

GORMANKOV, A. V. & S. V. MEYEN. 1986. Tatarina flora (composition, distribution in the Late Permian of Eurasia). Trudy Geol. Inst. Akad. Nauk S.S.S.R. 401 [in Russian].

GOULD, R. E. & T. DELEVORYAS. 1977. The biology of *Glossopteris*: Evidence from petrified seed-bearing and pollen-bearing organs. Alcheringia 1: 387–399.

GRAND'EURY, F. C. 1877. Mémoire sur la flore carbonifère du departement de la Loire et du centre de la France. Mém. Acad. Sci. Inst. France Ser. 2 24: 1–624.

GREGUSS, P. 1955. Identification of Living Gymnosperms on the Basis of Xylotomy. Akademiai Kiado, Budapest.

HAMER, J. J. & G. W. ROTHWELL. 1988. The vegetative structure of *Medullosa endocentrica* (Pteridospermopsida). Canad. J. Bot. 66: 375–387.

HARRIS, T. M. 1932a. The fossil flora of Scoresby Sound, east Greenland, Part 2. Description of seed plants *incertae sedis* together with a discussion on certain cycadophyte cuticles. Meddel. Grønland 85(3): 1–114.

———. 1932b. The fossil flora of Scoresby Sound, east Greenland, Part 3. Caytoniales and Bennettitales. Meddel. Grønland 85(5): 1–333.

———. 1933. A new member of the Caytoniales. New Phytol. 32: 97–114.

———. 1937. The fossil flora of Scoresby Sound, east Greenland, Part 5. Stratigraphic relations of the plant beds. Meddel. Grønland 113(2): 1–112.

———. 1940. *Caytonia*. Ann. Bot. 4: 713–734.

———. 1941. *Caytonanthus*, the microsporophyll of *Caytonia*. Ann. Bot. NS 5(17): 47–58.

———. 1962. The occurrence of the fructification *Carnocarnites* in New Zealand. Trans. Roy. Soc. New Zealand 4: 17–27.

———. 1964. The Yorkshire Jurassic Flora. II. Caytoniales, Cycadales and Pteridosperms. British Museum (Natural History), London.

———. 1969. The Yorkshire Jurassic Flora. III. Bennettitales. British Museum (Natural History), London.

HART, J. 1987. A cladistic analysis of conifers: Preliminary results. J. Arnold Arbor. 68: 269–307.

HERENDEEN, P. S., W. L. CREPET & K. C. NIXON. 1993. Chloranthus-like stamens from the Upper Cretaceous of New Jersey. Amer. J. Bot. 80: 865–871.

HILL, C. R. & P. R. CRANE. 1982. Evolutionary cladistics and the origin of angiosperms. Pp. 269–361 *in* K. A. Joysey & A. E. Friday (editors), Problems in Phylogenetic Reconstruction. Academic Press, New York.

HIRMER, M. 1933. Zur Kenntnis der structurbietende Pflanzenreste des jungeren Palaozoikums. I. Palaeontographica, Abt. B, Paläophytol. 77: 121–140.

HOLMES, W. B. K. 1987. New corystosperm ovulate fructifications from the Middle Triassic of eastern Australia. Alcheringia 11: 165–173.

JEFFREY, E. & R. TORREY. 1916. *Ginkgo* and the microsporangial mechanisms of the seed plants. Bot. Gaz. 62: 281–292.

KERP, J. H. F. 1988. Aspects of Permian palaeobotany and palynology. X. The west and central European species of the genus *Autunia* Krasser emend. Kerp (Peltaspermaceae) and the form-genus Rachiphyllum Kerp (callipterid folliage). Rev. Palaeobot. Palynol. 54: 249–360.

KIMURA, T. & S. SEKIDO. 1975. *Nilssoniocladus* n. gen. (Nilssoniaceae n. fam.) newly found from the early Lower Cretaceous of Japan. Palaeontographica, Abt. B, Paläophytol. 153: 111–118.

KRAUSEL, R. 1948. *Sturiella langeri* nov. gen. nov. sp., eine Bennettitee aus der Trias von Lunz (Nieder-Osterreich). Senckenbergiana 29: 141–149.

———. 1949. Koniferen und andere Gymnospermen aus der Trias von Lunz, Nieder-Osterreich. Palaeontographica, Abt. B., Paläophytol. 84: 35–78.

——— & F. SCHAARSCHMIDT. 1966. Die Keuperflora von Neuewelt bei Basel I. V. Pterophyllen und Taeniopteriden. Schweiz. Paläontol. Abh. 84: 1–64.

LES, D. 1988. The origin and affinities of the Ceratophyllaceae. Taxon 37: 326–345.

LIGNIER, O. 1894. Végétaux fossiles de Normandie. Structure et affinités du *Bennittites Morieri* (Sap. & Mar.) Mém. Soc. Linn. Normandie 18: 5–78.

LOCONTE, H. & D. W. STEVENSON. 1990. Cladistics of the Spermophyta. Brittonia 42: 197–211.

——— & ———. 1991. Cladistics of the Magnoliidae. Cladistics 7: 267–296.

LOGAN, K. J. & B. A. THOMAS. 1985. Distribution of lignin derivatives in plants. New Phytol. 99: 571–585.

LUCKOW, M. A. & R. A. PIMENTEL. 1985. Empirical comparisons of numerical Wagner computer programs. Cladistics 1: 47–66.

LUNDBLAD, A. B. 1948. On some *Caytonia*-like plant remains from the coal mines of Bjuv in Scania (Rhaetic). Svensk. Bot. Tidskr. 42: 84–86.

MACBRIDE, T. H. 1893. A new cycad. Amer. Geol. 12: 248–250.

MADDISON, W. P. & D. R. MADDISON. 1992. MacClade. Analysis of Phylogeny and Character Evolution. Version 3. Book and Software. Sinauer Associates, Sunderland, Massachusetts.

———, M. J. DONOGHUE & D. R. MADDISON. 1984. Outgroup analysis and parsimony. Syst. Zool. 33: 83–103.

MAPES, G. & G. W. ROTHWELL. 1980. *Quaestora amplecta* gen. et sp. n., a structurally simple medullosan

stem from the Upper Mississippian of Arkansas. Amer. J. Bot. 67: 636–647.

MARTENS, P. 1971. Les gnetophytes. Handb. Pflanzenanat. 12(2): 1–295.

MEACHAM, C. A. 1984. The role of hypothesized direction of characters in the estimation of evolutionary history. Taxon 33: 26–38.

———. 1986. More about directed characters: A reply to Donoghue and Maddison. Taxon 35: 538–540.

MEEUSE, A. D. 1963. From ovule to ovary: A contribution to the phylogeny of the megasporangium. Acta Biotheor. 16: 127–182.

MEYEN, S. V. 1984. Basic features of gymnosperm systematics and phylogeny as evidenced by the fossil record. Bot. Rev. 50(1): 1–111.

———. 1987. Fundamentals of Palaeobotany. Chapman & Hall, London & New York.

———. 1988. Gymnosperms of the Angara flora. Pp. 338–381 *in* C. B. Beck (editor), Origin and Evolution of Gymnosperms. Columbia Univ. Press, New York.

MEYER-BERTHAUD, B., E. L. TAYLOR & T. N. TAYLOR. 1992. Reconstructing the Gondwana seed fern *Dicroidium*: Evidence from the Triassic of Antarctica. Geobios 25: 341–344.

MICKEVICH, M. F. & J. S. FARRIS. 1982. Phylogenetic Analysis System (PHYSYS). Computer package published by the authors.

MILLAY, M. A. & D. A. EGGERT. 1970. *Idanothekion* gen. n., a synangiate pollen organ with saccate pollen from the Middle Pennsylvanian of Illinois. Amer. J. Bot. 57: 50–61.

——— & ———. 1974. Microgametophyte development in the Paleozoic seed fern family Callistophytaceae. Amer. J. Bot. 61: 1967–1075.

——— & T. N. TAYLOR. 1974. Morphological studies of Paleozoic saccate pollen. Palaeontographica, Abt. B, Paläophytol. 147: 75–99.

——— & ———. 1979. Paleozoic seed fern pollen organs. Bot. Rev. 45: 301–375.

MILLER, C. N. 1988. The origin of modern conifer families. Pp. 448–486 *in* C. B. Beck (editor), Origin and Evolution of Gymnosperms. Columbia Univ. Press, New York.

MUHAMMAD, A. F. & R. SATTLER. 1982. Vessel structure of Gnetum and the origin of angiosperms. Amer. J. Bot. 69: 1004–1021.

NATHORST, A. G. 1886. Om floran i Skånes kolförande bildingar. I. Floran vid Bjuf. Häfte 3. Sveriges Geol. Unders. Ser. C. No. 85. Stockholm.

———. 1909. Palaobotanische Mitteilungen, 8. Über *Williamsonia*, *Wielandia*, *Cycadocephalus* und *Weltrichia*. Kongl. Svenska Vetenskapsakad. Handl. 45(4): 1–38.

———. 1911. Pälaobotanische Mitteilungen. Kongl. Svenska Vetenskapsakad. Handl. 46: 1–33.

NIXON, K. C. 1989. Origins of Fagaceae. Pp. 23–43 *in* P. R. Crane & S. Blackmore (editors), Evolution, Systematics and Fossil History of Hamamelidae. Vol. 2. 'Higher Hamamelidae'. Oxford Univ. Press, Oxford.

———. 1993a. Clados Version 1.4. Published by the author, Trumansburg, New York.

———. 1993b. Dada Version 0.87. Beta. Published by the author, Trumansburg, New York.

——— & J. CARPENTER. In press. On outgroups. Cladistics.

——— & J. I. DAVIS. 1991. Polymorphic taxa, missing values, and cladistic analysis. Cladistics 7: 233–241.

——— & Q. D. WHEELER. 1991. Extinction and the origin of species. Pp. 119–143 *in* M. Novocek & Q. D. Wheeler (editors), Extinction and Phylogeny. Columbia Univ. Press, New York.

OLIVER, F. W. & D. H. SCOTT. 1904. On the structure of the Paleozoic seed *Lagenostoma lomaxi*, with a statement of the evidence upon which it is referred to *Lyginodenderon*. Trans. Roy. Soc. Edinburgh 197B: 193–247.

OSBORN, J. M., T. N. TAYLOR & P. R. CRANE. 1991. The ultrastructure of *Sahnia* pollen (Pentoxylales). Amer. J. Bot. 78: 1560–1569.

PANT, D. D. 1977. The plant of *Glossopteris*. J. Indian Bot. Soc. 56: 1–23.

——— & N. BASU. 1979. Some further remains of fructifications from the Triassic of Nidpur, India. Palaeontographica 168B: 162–178.

——— & D. D. NAUTIYAL. 1965. Seed-bearing *Ottokaria*-like fructifications from India. Nature 207: 623–624.

PEDERSEN, K. R. 1981. Some Mesozoic pteridospermous pollen-producing organs and pollen. 13. Int. Bot. Congr., Sydney, Australia. Abstracts: p. 190.

——— & E. M. FRIIS. 1986. *Caytonanthus* pollen from the Lower and Middle Jurassic. *In*: J. T. Møller (editor), Twenty Five Years of Geology in Aarhus. Geroskrifter Dept. Geol. Aarhus Univ. (Denmark) 24: 255–267.

———, P. R. CRANE & E. M. FRIIS. 1989. The morphology and phylogenetic significance of *Vardekloeftia* Harris (Bennettitales). Rev. Palynol. Palaeobot. 60: 7–24.

PHILLIPS, T. L., H. N. ANDREWS & P. G. GENSEL. 1972. Two heterosporous species of *Archaeopteris* from the Upper Devonian of West Virginia. Palaeontographica, Abt. B, Paläophytol. 139: 47–71.

PIGG, K. B. 1990. Anatomically preserved *Glossopteris* foliage from the central Transantarctic Mountains. Rev. Palaeobot. Palynol. 66: 105–127.

——— & T. N. TAYLOR. 1990. Permineralized *Glossopteris* and *Dicroidium* from Antarctica. Pp. 164–172 *in* T. N. Taylor & E. L. Taylor (editors), Antarctic Paleobiology—Its role in the Reconstruction of Gondwana. Springer-Verlag, New York.

——— & ———. 1993. Anatomically preserved *Glossopteris* stems with attached leaves from the central Transantarctic Mountains, Antarctica. Amer. J. Bot. 80: 500–516.

POORT, R. J. & J. H. F. KERP. 1990. Aspects of Permian palaeobotany and palynology. XI. On the recognition of true peltasperms in the Upper Permian of western and central Europe and a reclassification of species formerly included in *Peltaspermum* Harris. Rev. Palaeobot. Palynol. 63: 197–225.

QIN-ER, FU DE-ZHI YANG. 1993. A new morphological interpretation of the female reproductive organs in *Ginkgo biloba* L. with a phylogenetic consideration on gymnosperms. Acta Phytotax. Sin. 31: 294–296

RAO, A. R. 1976. Problems in Pentoxyleae. Palaeobotanist 25: 393–396.

———. 1981. The affinities of Pentoxyleae. Palaeobotanist 28–29: 207–209.

RENAULT, B. 1879. Structure comparée de quelque-

tiges de la flore carbonifère. Nouv. Arch. Mus. Hist. Nat., Sér. 2, 2: 213–348.

———. 1902. Sur quelques pollens fossiles. Prothalles males. Tubes polliniques, etc. du terrain houiller. Compt. Rend. Hebd. Séances Acad. Sci. 135: 229 234.

Retallack, G. J. & D. L. Dilcher. 1981. Arguments for a glossopterid ancestry for angiosperms. Paleobiology 7: 54–67.

Reymanówna, M. 1973. The Jurassic flora from Grojec near Krakow in Poland. Part II. Caytoniales and anatomy of *Caytonia*. Acta Palaeobot. 14: 45–87.

Rodin, R. 1967. Ontogeny of foliage leaves in *Gnetum*. Phytomorphology 17: 118–128.

Rothwell, G. W. 1972a. Pollen organs of Pennsylvanian Callistophytaceae (Pteridospermopsida). Amer. J. Bot. 59: 993–999.

———. 1972b. Evidence of pollen tubes in Paleozoic pteridosperms. Science 175: 772–774.

———. 1975. The Callistophytaceae (Pteridospermopsida): I. Vegetative structures. Palaeontographica, Abt. B, Paläophytol. 151: 171–196.

———. 1980. The Callistophytaceae (Pteridospermopsida): II. Reproductive features. Palaeontographica, Abt. B, Paläophytol. 173: 85 106.

———. 1981. The Callistophytales (Pteridospermopsida), reproductively sophisticated gymnosperms. Rev. Palaeobot. Palynol. 32: 103–121.

———. 1982. New interpretations of the earliest conifers. Rev. Palaeobot. Palynol. 37: 7–28.

———. 1988. Cordaitales. Pp. 273–297 *in* C. B. Beck (editor), Origin and Evolution of Gymnosperms. Columbia Univ. Press, New York.

——— & D. A. Eggert. 1986. A monograph of *Dolerotheca* Halle, and related complex permineralized medullosan pollen organs. Trans. Roy. Soc. Edinburgh 77: 47–79.

——— & S. Warner. 1984. *Cordaixylon dumusum* n. sp. (Cordaitales). I. Vegetative structures. Bot. Gaz. 145: 275–291.

Sahni, B. 1932. A petrified *Williamsonia* (*W. sewardiana*, sp. nov.) from the Rajmahal Hills, India. Palaeontologia Indica, Mem. Geol. Surv. India (new series) 20: 1–19.

———. 1948. The Pentoxyleae: A new group of Jurassic gymnosperms from the Rajmahal Hills of India. Bot. Gaz. 110: 47–80.

Scheckler, S. E. 1978. Ontogeny of progymnosperms II. Shoots of Upper Devonian Archaeopteridales. Canad. J. Bot. 56: 3136–3170.

Schimper, W. P. 1869. Traité de Paléontologie Végétale ou la Flore du Monde Primitif dans ses Rapports avec les Formations Géologiques et la Flore du Monde Actuel. J. B. Bailliere et fils, Paris.

Schopf, J. M. 1976. Morphologic interpretation of fertile structures in glossopterid gymnosperms. Rev. Palaeobot. Palynol. 21: 25–64.

Schoute, J. 1922. On whorled phyllotaxis. I. Growth whorls. Recueil Trav. Bot. Néerl. 19: 184–274.

———. 1925. On whorled phyllotaxis. II. Late binding whorls of *Peperomia*. Recueil Trav. Bot. Néerl. 22: 128–144.

Scott, D. H. 1912. The structure of *Mesoxylon lomaxii* and *M. poroxyloides*. Ann. Bot. (London) 26: 1011–1030.

Serlin, B. S. & H. P. Banks. 1978. Morphology and anatomy of *Aneurophyton*, a progymnosperm from the Late Devonian of New York. Palaeontogr. Amer. 8: 343–353.

Singh, H. 1978. Embryology of gymnosperms. Handb. Pflanzenanat. 10(2): 1–302.

Sitholey, R. V. & M. N. Bose. 1971. *Weltrichia santalensis* (Sith. & Bose) and other bennettitalean male fructifications from India. Palaeontographica, Abt. B, Paläophytol. 131: 151–159.

Srivastava, B. P. 1946. Silicified plant remains from the Rajmahal series of India. Proc. Nat. Acad. Sci. (India) 15: 185–211.

Steeves, T. A. & I. M. Sussex. 1989. Patterns in Plant Development. Cambridge Univ. Press, Cambridge.

Stevenson, D. A. 1974. The occurrence of "root gaps" in the rhizome, solenostele and leaf trace of *Dennstaedtia cicutaria*. Amer. J. Bot. 284–289.

———. 1988. Strobilar ontogeny in the Cycadales. Pp. 205–224 *in* P. Liens, S. C. Tucker & P. Endress (editors), Aspects of Floral Development. J. Cramer, Berlin.

———. 1990. Morphology and systematics of the Cycadales. Mem. New York Bot. Gard. 57: 8-55.

———. 1992. Formal classification of the extant cycads. Brittonia 44: 220–223.

———. 1993. Phylogenetic systematics of the cycads. Proc. Second Int. Conf. Cycad Biol., Palm and Cycad Society of Australia, Milton (in press).

Stewart, W. R. 1976. Polystely, primary xylem, and the Pteropsida. Birbal Sahni Inst. Paleobot., Lucknow.

——— & T. Delevoryas. 1956. The medullosan pteridosperms. Bot. Rev. 22: 45–80.

——— & G. W. Rothwell. 1993. Paleobotany and the Evolution of Plants. Cambridge Univ. Press, New York.

Stidd, B. M. 1981. The current status of medullosan seed ferns. Rev. Palaeobot. Palynol. 32: 63-101.

———. 1990. Further documentation of the structure of *Dolerotheca* and a critique of other theories. Palaeontographica, Abt. B, Paläophytol. 217: 51-86.

——— & J. W. Hall. 1970. Callandrium callistophytoides gen. et sp. nov., the probable pollen-bearing organ of the seed fern, Callistophyton. Amer. J. Bot. 57: 394-403.

Stopes, M. 1905. On the double nature of the cycadean integument. Ann. Bot. 19: 561 566.

Surange, K. R. & S. Chandra. 1975. Morphology of the gymnospermous fructifications of the *Glossopteris* flora and their relationships. Palaeontographica, Abt. B, Paläophytol. 149: 153-180.

Swofford, D. L. 1991. PAUP Version 3.0. Program and Documentation. Illinois Natural History Museum, Champaign, Illinois.

Sykes, M. 1910. The anatomy and morphology of the leaves and inflorescences of *Welwitschia mirabilis*. Philos. Trans., Ser. B 201: 179–226.

Takaso, T. 1980. A developmental study of the integument in gymnosperms 1. *Ginkgo biloba* L. J. Jap. Bot. 55: 14–27.

———. 1981. A developmental study of the integument in gymnosperms 2. *Pinus thunbergeri* Parl., *Abies mariesii* Mast. and *A. veitchii* Lindl. J. Jap. Bot. 56: 73–89.

———. 1984. Structural changes in the apex of the female strobilus and initiation of the female reproductive organ (ovule) in *Ephedra distachya* L. and *E. equisetina* Bge. Acta Bot. Neerl. 33: 257-266.

———. 1985. A developmental study of the integument in gymnosperms 3. *Ephedra distachya* L. and *E. equisetina* Bge. Acta Bot. Neerl. 34: 33–48.

——— & F. Bouman. 1986. Ovule and seed ontogeny in *Gnetum gnemon* L. Bot. Mag. (Tokyo) 99: 241–266.

——— & P. Tomlinson. 1989a. Aspects of cone and ovule ontogeny in *Cryptomeria* (Taxodiaceae). Amer. J. Bot. 76: 692–705.

——— & ———. 1989b. Cone and ovule development in *Callitris* (Cupressaceae–Callitroideae). Bot. Gaz. 150: 370–390.

——— & ———. 1990. Cone and ovule ontogeny in *Taxodium* and *Glyptostrobus* (Taxodiaceae–Coniferales). Amer. J. Bot. 77: 1209–1221.

——— & ———. 1991. Cone and ovule ontogeny in *Sciadopitys* (Taxodiaceae Coniferales). Amer. J. Bot. 78: 417–428.

——— & ———. 1992a. Seed cone and ovule ontogeny in *Metasequoia*, *Sequoia* and *Sequoiadendron* (Taxodiaceae–Coniferales). Bot. J. Linn. Soc. 108: 15–37.

——— & ———. 1992b. Aspects of cone morphology and development in Podocarpaceae (Coniferales). Int. J. Plant Sci. 153: 572 588.

Taylor, T. N. 1965. Paleozoic seed studies: A monograph of the American species of *Pachytesta*. Palaeontographica, Abt. B, Paläophytol. 117: 1–46.

———. 1971. *Halletheca reticulatus* gen. et sp. n.: Synangiate Pennsylvanian pteridosperm pollen organ. Amer. J. Bot. 58: 300–308.

———. 1988. Pollen and pollen organs of fossil gymnosperms: Phylogeny and reproductive biology. Pp. 177–217 *in* C. B. Beck (editor), Origin and Evolution of Gymnosperms. Columbia Univ. Press, New York.

——— & S. Archangelsky. 1985. The Cretaceous pteridosperms *Ruflorinia* and *Ktalenia* and implications on carpel and cupule evolution. Amer. J. Bot. 72: 1842–1853.

——— & D. A. Eggert. 1969. On the structure and relationships of a new Pennsylvanian species of the seed *Pachytesta*. Palaeontology 12: 382–388.

——— & M. A. Millay. 1981. Morphologic variability of Pennsylvanian lyginopterid seed ferns. Rev. Palaeobot. Palynol. 32: 27–62.

——— & W. N. Stewart. 1964. The Paleozoic seed *Mitrospermum* in American coal balls. Palaeontographica, Abt. B, Paläophytol. 115: 51 -58.

——— & E. L. Taylor. 1993. The Biology and Evolution of Fossil Plants. Prentice-Hall, Englewood Cliffs.

———, M. A. Cichan & A. M. Baldoni. 1984. The ultrastructure of mesozoic pollen: *Pteruchus dubius* (Thomas) Townrow. Rev. Palaeobot. Palynol. 41: 319–327.

Thomas, H. H. 1915. On *Williamsoniella*, a new type of bennettitalean flower. Philos. Trans., Ser. B 207: 113–148.

———. 1925. The Caytoniales, a new group of angiospermous plants from the Jurassic rocks of Yorkshire. Philos. Trans., Ser. B 213: 299–363.

———. 1933. On some pteridospermous plants from the mesozoic rocks of south Africa. Philos. Trans., Ser. B 222: 193–265.

———. 1958. *Lidgettonia*, a new type of fertile *Glossopteris*. Bull. Brit. Mus. (Nat. Hist.), Geol. 3: 179–189.

Tomlinson, P., T. Takaso & J. Rattenbury. 1989. Cone and ovule ontogeny in Phyllocladus (Podocarpaceae). Bot. J. Linn. Soc. 99: 209–221.

Townrow, J. A. 1962. On *Pteruchus* a microsporophyll of the Corystospermaceae. Bull. Brit. Mus. (Nat. Hist.), Geol. 6(2): 289–320.

Trivett, M. L. & G. W. Rothwell. 1985. Morphology, systematics, and paleoecology of Paleozoic fossil plants: *Mesoxylon priapi*, sp. nov. (Cordaitales). Syst. Bot. 10: 205–223.

——— & ———. 1988. Diversity among Palaeozoic Cordaitales: The vascular architecture of *Mesoxylon birame* Baxter. Bot. Gaz. 149: 116–125.

Troll, W. 1937. Vergleichende Morphologie der Hoheren Pflanzen. Bd. 1. Gebrüder Borntraeger, Berlin.

Vishnu-Mittre. 1953. A male flower of the Pentoxyleae with remarks on the structure of the female cones of the group. Palaeobotanist 2: 75–84, Plates 1–5.

Walker, J. W. & J. A. Doyle. 1975. The bases of angiosperm phylogeny: Palynology. Ann. Missouri Bot. Gard. 62: 664–723.

Wieland, G. R. 1906. American Fossil Cycads. Carnegie Inst., Washington.

Wilde, M. H. 1944. A new interpretation of coniferous cones I. Podocarpaceae (*Podocarpus*). Ann. Bot. (London) 8: 1–41.

Williamson, W. C. 1870. Contributions toward the history of *Zamia gigas* Lindl. & Hutton. Trans. Linn. Soc. London 26: 663–674.

Yao, X., T. N. Taylor & E. L. Taylor. 1992. Corystosperm pollen organs from the Triassic of Antarctica. OFP information 16-B, Organisation Internationale de Palaeobotanique IVème Conference, Paris. Abstracts: p. 178.

Zalessky, M. D. 1929. Observation sur quelques végéteaux fossiles nouveaux. Bull. Soc. Géol. France 29(3–5): 189–198.

Zavada, M. S. & W. L. Crepet. 1985. Pollen wall ultrastructure of the type material of *Pteruchus africanus*, *P. dubius* and *P. papillatus*. Pollen & Spores 27: 271–276.

——— & ———. 1986. Pollen wall structure of *Caytonanthus arberi* (Caytoniales). Pl. Syst. Evol. 153: 259–264.

Appendix A. Character list and discussion.

0. HABIT: woody (0); herbaceous (1); submerged-aquatic (2); additive.

Previous investigators (e.g., Loconte & Stevenson, 1990) have segregated shrub and tree habit (see character 0). We prefer to combine these two conditions as a single state "woody" because the distinction between tree and shrub is at best arbitrary, difficult in practice, and often polymorphic within angiosperm terminals. Woody is understood here to include a woody growth form derived from the presence of a bi-directional vascular cambium that produces secondary xylem centripetally and secondary phloem centrifugally. Consequently the monocots are not considered woody. However, the anomalous growth patterns of such taxa as the medullosans, *Pentoxylon*, and some cycads (Stevenson, 1990) are considered woody because each of the "steles" in their stems does have a complete vascular cambium as described above and produces secondary wood that can be considered in terms of

wood anatomical features, as discussed below under wood anatomy. This is also applicable to the supernumery cambia that occur in some cycads as well as in *Gnetum*. The herbaceous and submerged aquatic growth habits are not known to occur in taxa in this analysis outside of the angiosperms. Logically, because all known submerged aquatics in our analyses are herbaceous (nonwoody), we have encoded character 0 as additive (ordered).

1. AXILLARY BUDS: absent (0); simple (1); multiple (2); additive.

Although this character is coded in terms of the presence of axillary buds, it is equivalent to the "branching dichotomous" versus "branching axillary" character of some previous analyses. The character is encoded as additive (ordered) under the assumption that multiple buds are derived. It should be noted that a nonadditive coding does not change our results. Dichotomous branching as used here includes both isotomous and anisotomous patterns. In some angiosperms, both axillary and dichotomous branching are known to occur in the same plant, but these instances are found in what we assume to be highly derived angiosperms such as some cacti (Troll, 1937; Boke, 1976) and some monocots (Fisher, 1973, 1976). Some cacti even have multiple buds in addition to dichotomous and axillary branching states (Troll, 1937). In all cases of dichotomous branching within the angiosperms, the taxa involved also express axillary branching in the same plants. All of the angiosperm terminals used in our analyses branch in axillary fashion.

Recently, it has been suggested by Doyle & Donoghue (1992) that dichotomous branching in extant cycads is derived from axillary branching. This conclusion is based upon the external morphology of the lower cretaceous fossil of the putative cycad *Nilssoniocladus* (Kimura & Sekido, 1975) and putative axillary branching in *Lyginopteris* and medullosans. In the case of *Lyginopteris*, the evidence that has been presented (Galtier & Holmes, 1982) is equivocal, and branching in *Lyginopteris* appears to be similar to the adventitious branching found on the petiole bases of extant dennstaediod ferns, based on position and vascular organization (Stevenson, 1974). In the case of the medullosans, only one species, *Medullosa endocentrica*, has been reported as having axillary branching (Hamer & Rothwell, 1988). This points to the problem of scoring reconstructions based on different form genera, and the problem of synthate taxa based on assumptions of relatedness. We have thus coded both our medullosan and lyginopterid terminals as uncertain (ambiguous) for the character of axillary branching.

According to Kimura & Sekido (1975), the inclusion of *Nilssoniocladus* within the cycads is based upon straight epidermal cell walls and the presence of haplocheilic stomata. Both of these characters are plesiomorphic within seed plants, based on several recent analyses as well as traditional concepts; therefore, the presence of these characters in a fossil cannot exclusively nor conclusively indicate cycadalean affinity. In fact, *Nilssoniocladus* has no synapomorphies with either extant or known extinct cycads. The short-shoot morphology and simple leaves of *Nilssoniocladus* are not known for extant cycads or any fossils that share synapomorphies with the cycads. There is no axillary branching evident in the earliest unequivocal cycads, *Crossozamia chinensis* Zhu & Du and *Tianbaolinia circinalis* Gau & Thomas from the Early Permian of China (Gao & Thomas, 1989), which are virtually indistinguishable from the extant genus *Cycas*. Because we find no evidence to support axillary branching as occurring in either fossil or extant cycads (Stevenson, 1988), we have maintained the position of Loconte and Stevenson and scored all cycad taxa as lacking axillary buds (state 0).

2. SHORT SHOOTS: absent (0); present (1).

Short shoots are defined as lateral shoots that differ in morphology from main shoots by suppression/reduction of internodes (as in *Ginkgo*).

3. APICAL MERISTEM: w/o tunica (0); w/tunica (1).

The concept of tunica-corpus organization of shoot apical meristems has been discussed by Loconte & Stevenson (1990) and Doyle & Donoghue (1992). The character as treated here is equivalent. However, as discussed by Loconte & Stevenson (1990) we consider the corpus and the lack of a tunica to be vascular plant plesiomorphies and the presence of a tunica to be apomorphic. The plesiomorphic presence of the corpus in the seed plants is not a semantic issue as suggested by Doyle & Donoghue (1992). Rather, it is a necessary part of the stem apical growth in the seed plants, and its presence is supported not only by histology but also by cytohistochemistry and cell division patterns in terms of maintaining the conical shape of the meristem (Gifford & Corson, 1971; Steeves & Sussex, 1989).

4. STELE: protostele (0); eustele (1); polystele (2); nonadditive.

The common condition throughout extant seed plant groups is eustelar organization. Among the terminals used in our analyses, *Ceratophyllum* has a protostele, as found in many (apparently unrelated) submerged aquatic angiosperms such as *Mayaca*. Given the probable phylogenetic position of these taxa, the protostelic condition of certain aquatic angiosperms is almost certainly derived from the eustelic condition. Some members of the Cycadales have a polystelic condition similar to that found in many medullosans (Stevenson, 1990). We have also scored *Pentoxylon* as having a polystele although it differs from that found in the cycads and medullosans in anatomical details (see sections on fossil groups).

5. NODAL ANATOMY: 1-trace unilacunar (0); 1-trace per bundle (1); multilacunar (2); 2-trace unilacunar (3); trilacunar (4); nonadditive.

Nodal anatomy is scored as in Loconte & Stevenson (1990). This character as scored in Doyle & Donoghue (1992) is a composite character of petiole anatomy and nodal anatomy and as such excludes certain possible combinations. This would be particularly true if one were to include ferns in an analysis. This character should be limited to the number of departing traces as related to the number of supplying bundles in the stem. For example, Doyle & Donoghue (1992) considered that cycads have a number of traces derived from a solid arc of xylem. Our observations do not confirm this. The leaf trace system of cycads is derived from numerous small bundles that only appear as a solid arc after the production of secondary xylem has obscured the integrity of the primary vascular system (Chamberlain, 1935). We have therefore scored all three cycad terminals as state 2 (multilacunar). In contrast, the vascular pattern of the petiole in cycads reflects the division of bundles in the cortex of the stem.

Thus, the number of bundles departing from those of the stem is not directly related to the number or arrangement in the petiole. In fact, the number of departing traces does not even represent a minimum number because of anastomoses that may occur in the cortex. Also, the anatomy of departing traces does not necessarily match that of the leaf traces (see discussion under character 24—leaf trace xylem).

6. GIRDLING LEAF TRACES: absent (0); present (1).

Girdling leaf traces (with multilacunar nodal anatomy) are known only from the extant and fossil Cycadales, and thus this character is a synapomorphy for the Cycadaceae, Stangeriaceae, and Zamiaceae (Stevenson, 1990).

7. PRIMARY XYLEM: mesarch (0); endarch (1).

Primary xylem character (7, 8) states are described for fossil taxa under those entries. All of the extant taxa in this study have endarch primary xylem (character 7).

8. PRIMARY XYLEM PITS: scalariform (0); conifer type (1).

This character is the same as used in Doyle & Donoghue (1992) and various previous analyses; data are derived in large part from Greguss (1955) and Bierhorst (1971).

9. WOOD: manoxylic (0); pycnoxylic (1).

Basically the same as used by Loconte & Stevenson (1990) and Doyle & Donoghue (1992). Data for manoxylic versus pycnoxylic xylem are derived from Greguss (1955) and descriptions of fossil taxa in the literature (see Stewart & Rothwell, 1993; Taylor & Taylor, 1993, and references cited therein).

10. SECONDARY XYLEM PITS: scalariform (0); mixed (1); circular (2); additive.

Secondary xylem pitting is considered to refer only to the lateral walls of the tracheary elements of the secondary xylem and is treated as an additive multistate character. The state "mixed" refers to the presence of individual tracheary elements that have both scalariform and circular pits. We have scored this as an additive character to avoid problems of the polymorphic "mixed" condition. The additivity of the character is consistent with allowing a polymorphic stage to be intermediate between two endpoints; it also maintains grouping information that is lost if "mixed" is scored as an independent state in a nonadditive character. Of course, the co-occurrence of both circular and scalariform pits suggests that, while there may be ecological and/or conceptual reasons to associate these in the same character, they may be independent characters. Because there are no terminals that lack both scalariform and circular pits, treating this character as we have above is logically and computationally identical to scoring two separate binary presence-absence characters for scalariform and circular pits.

11. XYLEM RAYS: uniseriate/biseriate (0); some multiseriate (1).

Basically the same as used by Loconte & Stevenson (1990) and Doyle & Donoghue (1992). Data are derived mostly from Greguss (1955) and descriptions of fossil taxa in the literature (see Stewart & Rothwell, 1993; Taylor & Taylor, 1993; and references cited therein). Some data are also derived from standard wood references such as Brown & Panshin (1934).

12. VESSELS: absent (0); present (1).

In order to reduce bias due to preconceived notions about the evolution of vessel elements (in particular perforation plates), we have separated the form of the perforation plate (character 13) from whether or not vessels occur. This assumes that angiosperms (scalariform) and gnetopsid (foraminate) vessels are homologous; see Muhammad & Sattler (1982) for a discussion of the similarity of gnetopsid and angiosperm vessel elements.

13. VESSEL PERFORATIONS: foraminate (0); scalariform (1).

See Muhammad & Sattler (1982) for a discussion of this character in *Gnetum*. The simple perforations of some angiosperms (e.g., *Chrysolepis*) were assumed to be derived from, and therefore were scored as, scalariform. Adding the third state "simple" would provide little if any grouping information in our analyses, but would be useful in an expanded analysis that included more angiosperms.

14. SIEVE TUBE PLASTIDS: s-type (0); p-type (1).

As used in numerous previous analyses. We were not able to utilize subclasses of the two types of plastids. Data are from Behnke (1988) and references cited therein.

15. COMPANION CELLS: absent (0); present (1).

As defined by Loconte & Stevenson (1990) and Doyle & Donoghue (e.g., 1992).

16. LIGNIN SUBUNITS: vanillin (0); syringal groups (1).

Data for vanillin versus syringal subunits of lignin are from Logan & Thomas (1985). Only known for extants; the chemical assay of lignin type (Mäule reaction) requires intact wood.

17. CORTICAL SECRETORY STRUCTS: absent (0); cavities (1); canals (2); nonadditive.

Data are from Bierhorst (1971), Taylor & Taylor (1993), and from unpublished observations. Secretory cavities are areas in parenchymatous tissue where there are independent lacunae that are lined with secretory epithelial cells. In contrast, secretory canals are longitudinal structures that form a network of lacunae that are lined with epithelial cells. In both cases, the lacunae are schizo-lysigenous in origin. Cortical secretory structures vary independently from secretory structures that often occur in secondary xylem or rays. Thus, taxodiaceous and cupressaceous mature woods lack secretory canals, but canals are present in the cortical tissues of young stems. This three-state character has been treated as unordered because there is no direct evidence that canals are derived from cavities.

18. ETHEREAL OIL CELLS: absent (0); present (1).

Ethereal oil cells (as far as known) are limited to angiosperms. The cells that produce ethereal oils are specialized parenchyma cells. Data are from Cronquist (1981).

Loconte & Stevenson (1991), and general taxonomic references.

19. RESINS: absent (0); present (1).

Although resins are the products of secretory structures, there is not a one-to-one correlation between type of secretory structure (e.g., canal or cavity) and the type of secretion (e.g., resin or mucilage). The presence of these resins is limited in seed plants to extant and extinct conifers (but conspicuously absent from cordaitalean taxa) and corystosperms. It should be noted that while conifers have resin-secreting canals, the corystosperms have resin-secreting cavities (dealt with in character 18). In the same manner, the cycads, medullosans, and cycadeoids have non-resin secreting canals (mucilage in the cycads), whereas *Ginkgo*, *Callistophyton*, *Lepidopteris*, *Tatarina*, and *Glossopteris* have secretory cavities that do not produce resins (at least these have not been detected in the above fossils).

20. PHYLLOTAXY: alternate (0); opposite or whorled (1).

Phyllotaxy is treated as either alternate or opposite/whorled. As have previous workers, we have treated whorled leaves as a subset of opposite; such treatment is supported by the common association of the two states in disparate groups, as in the case of *Ephedra* where some species have opposite leaves and others have whorls of three leaves at each node. Pseudowhorls or pseudo-opposite phyllotaxy are often difficult to recognize, as is the case in *Catalpa* and *Peperomia* (Schoute, 1922, 1925). Of the taxa used in our analyses, perhaps the most problematic is *Platanus*, which we have scored as alternate (the traditional interpretation), but which may in fact be derived independently through sympodial branching and reduction of one leaf at each node to become the foliar "stipule" that encircles the stem, much as the leaf base encircles the axillary bud.

21. LEAF BASE: simple (0); sheathing (1).

Because of difficulty in scoring early developmental stages in fossil taxa, we have restricted our definition of "sheathing" leaf base to those taxa which express the condition in mature leaves. Thus, those taxa that appear to have sheathing leaves during early ontogeny such as in the cycads (Stevenson, 1990), but do not have sheathing leaves at leaf and stem maturity, are scored as having simple leaf bases.

22. STIPULES: absent (0); present (1).

Stipules are considered here to be the presence of appendages associated with the leaf base. These may be borne on the leaf base, petiole, or adjacent parts of the stem. The character is limited in distribution to some angiosperms and some cycads (Stevenson, 1990). Because of the diverse nature of these structures, it is unlikely that all stipules are homologous; the character has been retained here only tentatively until more detailed comparative analyses of "stipular" structures can be developed.

23. LEAF TRACE XYLEM: mesarch (0); endarch (1).

We have introduced a new character dealing with endarch versus mesarch (including exarch) leaf traces. This character is not strictly correlated with the xylem pole position in stem bundles as might be supposed. For example, the cycads have endarch stem bundles with mesarch leaf traces (Stevenson, 1990).

24. LEAVES: simple (0); compound (1).

While a few fossil taxa are difficult to score, this is a fairly straightforward character.

25. PRIMARY VEIN FORM: dichotomous (0); anisotomous (1); solitary/unbranched (2); nonadditive.

This character refers to the primary vein system only, and thus avoids the problem of scoring "midvein dichotomous" in one taxon, and midvein "not dichotomous" in taxa such as *Ginkgo* with only one order of veins.

26. LEAF VENATION: parallel (0); pinnate (1); palmate (2); nonadditive.

This character was coded only for taxa with more than one order of venation, or in the case of parallel venation, those with multiple primary veins (e.g., *Ephedra*). Taxa such as conifers and *Ginkgo* were coded as inapplicable (−) because the primary vein form character adequately describes the leaf venation.

27. VEIN ORDERS: one (0); two (1); three or more (2); additive.

All taxa in our analyses have at least one order of venation. Two vein orders occur by branching off from the primary midvein (e.g., *Gnetum* and most angiosperms) or parallel primary veins (e.g., *Welwitschia* and monocots). This character was scored as additive because of the logical dependence of states 1 and 2 (if a leaf has three orders of veins, it by definition has two as well). Size classes of veins were used, and the rachis of certain compound leaves was considered to be the "primary" vein (as was implicit in the codings of some leaf characters in Doyle & Donoghue, 1986a, b, 1987).

28. LAMINAR VEIN FORM: dichotomous (0); anisotomous/non-dichotomous (1).

Laminar vein form refers to the pattern of venation in leaves with more than one order of veins; it is not scored (inapplicable) in those taxa with only one order of veins (e.g., *Ginkgo*) because the form of the primary vein in such taxa has already been described in character 25. Based upon developmental studies (Rodin, 1967) it is clear that *Gnetum* has an angiosperm-like venation pattern based upon a system of anisotomous branching rather than the common monopodial pattern of the angiosperms.

29. VEIN FUSION: nonanastomosing (0); anastomosing (1).

Vein fusions occur in those forms that are dichotomous and anastomosing (e.g., *Encephalartos* and *Gnetum*) as well as nondichotomous anastomosing forms in angiosperms. In some taxa, anastomoses occur only near the margins of leaves (e.g., *Ginkgo*) and do not occur consistently throughout the lamina. In such cases, the taxa were scored as nonanastomosing because the anastomoses are not consistent throughout the lamina or from leaf to leaf. The character therefore is defined as anastomoses consistently distributed over the leaf blade.

30. CHLORANTHOID TEETH: absent (0); present (1).

This character has been used in previous within-angiosperm analyses (e.g., Donoghue & Doyle, 1989). We note, however, that in that analysis assumptions were made about plesiomorphic states within the "hamamelid" terminal.

31. GUARD CELL POLES: raised (0); level (1).

This character and character 32 have been used routinely in seed plant analyses (e.g., Crane, 1985; Doyle & Donoghue, 1987, 1992; Loconte & Stevenson, 1990). We note that it is difficult to determine with certainty in some fossil material.

32. STOMATES: haplocheilic (0); some or all syndetocheilic (1).

See Doyle & Donoghue (e.g., 1987).

33. ASTROSCLEREIDS IN LEAF: absent (0); present (1).

The definition and scoring of this character follows that of Loconte & Stevenson (1991).

34. STROBILI: unisexual (0); bisexual (1); functionally unisexual (2); additive.

This character refers to the sex of whole strobilar axes. By definition, all dioecious plants are unisexual, regardless of the interpretation of what constitutes a strobilus. Scoring of some taxa is of necessity dependent on the interpretation of "strobilus" but in practice there seems to be little difficulty, and our interpretations are generally consistent with previous analyses. The angiosperm flower is here considered to represent a bisexual strobilus. Under the assumption that functionally unisexual strobili with vestigial parts of one sex (e.g., fertile microsporophylls and a sterile ovule, as in *Welwitschia*) are derived from bisexual axes, we have encoded this character as additive.

35. PERIANTH: absent (0); present (1).

The perianth is here operationally defined as a set (whorl or spiral) of sterile appendages subtending carpels and/or stamens; because of uncertain homology we have not scored the gnetopsids or cycadeoids as possessing a perianth. The bracts subtending the strobilus of cycadeoids, while prominent, are no more definitively homologous to the angiosperm "perianth" than are the often sterile bracts in the lowermost portion of the strobili of some Pinaceae. Until more certain homology of reproductive structures of gnetopsids, angiosperms, and cycadeoids can be postulated, it seems unwise to declare homology in some parts of the "strobili" when positional relations of parts are unknown; characters such as "perianth" are homologous only by their positional relation to carpels, which are unknown (or unrecognized) outside of the angiosperms.

36. MICROSPOROPHYLL: pinnate (0); simple (1).

We interpreted angiospermous stamens as microsporophylls; there is a long history of other interpretations (e.g., such as diphyllous structures, peltate structures; see Eames, 1961). In general, outside the angiosperms, microsporophylls were interpreted as planate or laminar structures to which microsporangia (or synangia) are attached. Our interpretations have in general followed traditional lines. In those cases where the attachment and nature of pollen-bearing organs is uncertain (e.g., medullosans) these characters are scored as ambiguous (see also section on medullosans).

Based upon the extensive studies of Martens (1971, and literature cited therein), *Ephedra* and *Welwitschia* are scored as having pinnate microsporophylls instead of simple microsporophylls as they have been scored in some previous analyses. In *Welwitschia*, the six "simple" microsporophylls (as interpreted by Doyle & Donoghue, 1986a, b, 1987, 1992) are supplied by two vascular traces, each of which branches to supply three "simple" appendages (Sykes, 1910). Each of these groups of three are characterized by a larger appendage (the central one) and two smaller lateral appendages; in early stages of development (Martens, 1971) these can be clearly seen as two opposite three-lobed structures; further evidence that these are indeed two opposite structures is found in their position relative to subtending bracts, which are decussate; if interpreted as two opposite three-lobed structures, the microsporophylls continue perfectly the decussate taxis of the strobilus; this taxis then continues *above* the two microsporophylls in the two sterile bracts enveloping the sterile central ovule (Martens, 1971). The clearly oppositely arranged three-pinnate microsporophylls of *Welwitschia* have been widely interpreted as six simple sporophylls that are basally fused (e.g., Crane, 1985; Doyle & Donoghue, 1986a, b, 1987, 1992). Likewise, the evidence is strong that microsporophylls of *Ephedra* are opposite or whorled compound (pinnate) structures that are partially or completely fused. *Gnetum* appears to have opposite, connate simple sporophylls; an obvious interpretation is that these are reduced from compound sporophylls of a cycadeoid or *Welwitschia* type.

Within angiosperms, we have followed tradition and encoded all taxa as having simple microsporophylls; however, it is worth pointing out that *Chloranthus* might as easily be interpreted as having (in some species) three-lobed pinnate microsporophylls as opposed to the traditional interpretation that these are three simple stamens that have migrated together, become fused, and the two lateral ones are reduced in size (see Herendeen et al., 1993 for a discussion of the various interpretations of *Chloranthus* stamens and their implications). If the chloranthoid stamens are interpreted as compound pinnate structures, the reduced lateral "glands" found at the base of many Lauralean stamens might also be interpreted as reduced lateral pinnae of a chloranthoid pinnate microsporophyll. We have not encoded any such interpretations in our matrix, but hope that further investigation of angiosperm taxa as well as gnetopsids may provide evidence to support or refute the existence of pinnate microsporophylls within angiosperms. Certainly the presence of pinnate microsporophylls in both commonly accepted outgroups to angiosperms (cycadeoids and gnetopsids) makes the existence of pinnate structures in angiosperms, if not likely, at least not surprising.

37. MICROSPOROPHYLLS: spiral (0); whorled/opposite (1).

This is a straightforward character, except in certain fossil groups such as the glossopterids (due to missing parts or difficulty in determining homology). It should be noted that in Doyle & Donoghue (1986a, b, 1987, 1992), the single angiosperm terminal was scored as having spiral

microsporophylls; in our analysis, by scoring numerous angiosperm taxa as observed, we allow parsimony to select the likely ancestral state for angiosperms.

38. MICROSPOROPHYLLS: free (0); basally fused (1).

This is a difficult character to score within angiosperms in some cases, particularly when fusion of parts such as the calyx and carpels may envelop the basal portion of stamens.

39. MICROSPORANGIA PER UNIT: many (0); 1–4 (1).

This character refers to the number of microsporangia per ultimate appendage, or sporangia-bearing "unit." This means that taxa such as medullosans can be scored because detached pollen organs provide at least a minimum number.

40. MICROSPORANGIA: terminal (0); marginal (1); adaxial (2); abaxial (3); nonadditive.

This character is similar in definition and scoring to one used in previous seed plant analyses; we note some difficulty in interpreting angiosperm taxa when the stamen form is filamentous and there is not a clear development of a connective extension (in our analyses, few such taxa were included, but with expanded analyses, this may pose a problem). The "peltate" theory for the origin of the angiosperm stamen (see Eames, 1961) is also germane to this character, for, if such an interpretation is accepted, then all angiosperm stamens are basically terminal (as in gnetopsids) and are modified developmentally to be marginal, abaxial, etc. We stand neutral on this issue, and prefer to score the character based on observation, not models of evolutionary transformation.

41. MICROSPORANGIA: free (0); fused at least basally (1).

This character is defined in the same manner as previous analyses; we find it difficult to score with certainty in numerous taxa, and our matrix reflects this.

42. MICROSPORANGIAL DEHISCENCE: ectokinetic (0); endokinetic (1); endothecial (2); nonadditive.

The concept of ectokinetic versus endokinetic microsporangial dehiscence was first introduced by Jeffrey & Torrey (1916). The ectokinetic mechanism is derived from epidermal cells, as in cycads, whereas the endokinetic system is derived from two or more subepidermal cell layers without epidermal differentiation, as in *Ginkgo*. We have introduced this character here and added a further state, endothecial, which is a subset of endokinetic, that utilizes only one subepidermal layer, the hypodermal layer. Scoring is based upon observations of extant and fossil taxa (Stevenson, unpublished). Further data are from Singh (1978) for many conifers and Martens (1971) for many gnetopsids.

43. MICROSPORE (POLLEN) SYMMETRY: radial (0); bilateral (1).

Pollen symmetry has been used previously; it is relatively straightforward, although in some instances the collapse of globose radial grains could produce a bilateral-appearing grain. Thus, all scores are based upon uncollapsed grains.

44. MICROSPORE TETRAD SCAR: present (0); absent (1).

Tetrad scars (character 47) are found only in fossil taxa in our analyses and the character is discussed under those entries. It is interesting to note that medullosans have both a proximal tetrad scar and a distal aperture; this supports the distinction between characters of the aperture and the tetrad scar.

45. MICROSPORE APERTURES: inaperturate (0); polar monoaperturate (1); equatorial multiaperturate (2); nonadditive.

This character has been used in some form in previous analyses; by scoring several angiosperms, we have not presumed their ancestral state. State 2, "equatorial multiaperturate," encompasses mostly triaperturate (tricolpate and tricolporate) taxa. Within angiosperms, character 47 below deals with variation within the tricolpate/tricolporate/triporate forms.

46. LEPTOMATE APERTURE: absent (0); present (1).

The "leptoma" is a distal rather indistinct germination pore (thin area in the wall) found in Cordaitalean and extant conifer pollen; it is more radially symmetrical in shape than the typical elongate sulcus of most monosulcate pollen.

47. COLPUS FORM: colpate (0); colporate (1); pororate (2); additive.

This character is scored as additive based on the compound nature of the apertures in the triporate taxa included in our analyses (e.g., *Betula*). All monoaperturate and inaperturate pollen is scored as inapplicable to avoid unjustified weighting of the equatorial/multiaperturate character.

48. POLLEN SACCUS: non-saccate (0); saccate (1).

This character has been used in all previous seed plant analyses in a similar manner. See also character 49.

49. SACCUS FORM: eusaccate (0); quasisaccate (1).

Pedersen & Friis (1986) observed a denser, infilled (endoreticulate) saccus interior, or "quasisaccate" condition, in pollen of *Caytonanthus*; similar pollen is attributed to glossopterids and corystosperms (Taylor & Taylor, 1993). This may indicate multiple origins of saccate pollen or transformations within homologous saccate pollen types.

50. EKTEXINE STRUCTURE: alveolar or ramifying (0); granular/columellate (1).

Some variant of this character has been widely used in previous analyses. Because of difficulty in distinguishing categories of alveolar, honeycomb, ramifying, and various "solid" types of pollen, as well as a very confounded and inconsistent literature, we have chosen to lump ektexine structure for all of those putatively "primitive" types and differentiate only the granular, columellate forms as found in cycadeoids, gnetopsids, and angiosperms.

51. ENDEXINE STRUCTURE: lamellate (0); granular (1).

Previously used in seed plant analysis; our coding follows those. We should point out, however, that while all angiosperms are coded as having granular endexine, layered endexine is known especially in the zone of apertures, and perhaps this character needs to be reevaluated to take this into account.

52. TECTUM: absent (0); clearly defined (1).

As we define the tectum, it is a clearly consolidated outer layer of the ektexine; thus, we do not consider the loosely associated outer granular layer of some coniferophyte pollen to be tectate.

53. TECTUM STRUCTURE: columellate (0); granular or solid (1).

For those taxa that have tectate pollen, we have scored whether the tectum is underlain by columellae or granular/solid structure. In the case of *Betula* and *Casuarina*, we scored the granular/columellate wall as columellate.

54. TECTUM FORM: continuous or foveolate (0); semitectate or reticulate (1).

Scored only for tectate pollens. Terminology follows that of Walker & Doyle (1975).

55. PARALLEL EXINE STRIATION: absent (0); global (1); proximal (2); nonadditive.

Gross similarity in exine morphology has been noted between the glossopterids and *Ephedra* and *Welwitschia*; the "parallel" exine striations of these taxa, however, differ in their distribution and orientation (globally distributed in the gnetopsids and restricted to the cappus in glossopterids). Various striate pollen types of some angiosperms are not considered homologous with either of these types that are fundamentally supratectal in nature, although some taxa of striate angiosperms (e.g., certain Lauraceae) need investigation.

56. MICROGAMETOPHYTE: more than 4-nucleate (0); 4-nucleate (1); 3-nucleate (2); additive.

This character has been widely used in seed plant analyses; we encode it as additive under the assumption that reduced 4- and 3-nucleate types are part of a reduction series; other arguments for additive coding can be made on the basis of meristic logic.

57. POLLEN TUBE: suspended (0); penetrating (1).

The differences and significance of penetrating versus suspended pollen tubes are discussed in Loconte & Stevenson (1990). This character would appear to be correlated with motile versus nonmotile male gametes, as pointed out by Doyle & Donoghue (1992), but the latter is only known for extant taxa, and thus complete correlation is not known. The presence or absence of flagellate male gametes as dependent upon the presence or absence of penetrating pollen tubes is not necessarily dependent upon the latter just as ramiform pollen tubes are not dependent upon gamete motility.

58. RAMIFORM POLLEN TUBES: absent (0); present (1).

Ramiform pollen tubes occur in cycads, *Ginkgo*, and conifers but are not known in gnetopsids. With the exception of *Callistophytales*, the nature of pollen tubes is not known in fossil seed plants. Within angiosperms, branched pollen tubes appear to be correlated with chalazogamy in some hamamelidid groups (Eames, 1961); however, these data are spotty and inconsistent.

59. STALK CELL: present (0); absent (1).

The stalk cell is the sterile derivative of the antheridial cell in the male gametophyte (Singh, 1978). As pointed out by Singh, this cell should probably be called the "secondary prothallial cell," but historical usage is retained here. A stalk cell is found in the endosporic microgametophyte of the vascular cryptograms, cycads, conifers, and *Ephedra* (Singh, 1978). We have scored this character as unknown for all fossils, although the form of the male gametophyte in fossil Callistophytaceae (Millay & Eggert, 1974) indicates that it is probably present in this group.

60. SPERM: flagellate (0); nonflagellate (1).

All vascular cryptograms have flagellate sperm. In extant seed plants, flagellate sperm that are structurally more complex than those of cryptogams occur in cycads and *Ginkgo*. The remainder of extant seed plants are nonflagellate, and their nonmotile sperm are sometimes referred to simply as "male cells" (e.g., Singh, 1978). Lack of preservation prevents scoring this character for fossil taxa.

61. SIMPLE MEGASTROBILUS: absent (0); present (1).

62. COMPOUND MEGASTROBILUS: absent (0); present (1).

Characters 61 and 62 are logically connected, since all compound strobili by definition are made up of simple strobili; by separating the two components, we were able to code certain fossil taxa (e.g., *Caytonia*) as having *at least* simple strobili (determinate reproductive axes) without making decisions on how these detached organs might have been organized into compound axes. We define strobilus in this context as a determinate reproductive axis bearing fertile appendages; a "compound" strobilus is mostly a matter of branching order. With the exception of our reinterpretation of certain fossils (e.g., *Caytonia* and *Corsytosperms*) our scoring of this character is similar to that of previous analyses.

Cycas, with its alternating production of ovule-bearing structures with vegetative leaves on the same axis, does not have strobilar structure, and therefore is scored as lacking a simple megastrobilus. Medullosans, *Lyginopteris*, *Archaeopteris*, and *Callistophyton* are considered not to have a simple megastrobilus because the ovule-bearing structures are produced on what appear to be indeterminate stems in a manner similar to *Cycas* (see section on fossil taxa).

In some taxa that have a simple megastrobilus, e.g., Taxaceae, it is not clear if a compound strobilus is present, and such taxa have been scored as ambiguous. The work of Eames (1952), Martens (1971), Takaso (1984, 1985), and Takaso & Bouman (1986) clearly demonstrates the presence of a compound strobilus in the gnetopsids.

The "compound" nature of the microstrobilus of gne-

topsids might be considered a synapomorphy of the gnetopsid clade. We have not encoded a character for simple versus compound microstrobilus (as suggested by one anonymous reviewer). Given the uncertainty in interpretation of angiosperm floral homology, it is not possible to score angiosperm "microstrobili" (flowers) as unambiguously compound or simple; moreover this character has no effect on our results, because, if the angiosperms are coded as uncertain (as they should be), it is equally parsimonious for gnetopsids to be monophyletic or paraphyletic to an angiosperm clade. Within the conifer clade, some taxa are problematic in regard to this character, and at least some species of *Podocarpus* have what have been interpreted as compound microstrobili (Wilde, 1944). Additionally, numerous fossil taxa in our analysis would be unknown for the microstrobilus character.

63. WOODY CONES: absent (0); present (1).

The presence or absence of woody cones is limited to three conifer families and Cordaitales.

64. COMPOUND CONE UNITS: many (0), few (1).

This character reflects the degree of branching in compound cones and is of value only within the conifer clade.

65. CARPEL: absent (0); present (1).

The term carpel is used here in the classical sense (Gifford & Foster, 1988) and is considered to be an angiosperm synapomorphy. The homology of this structure with any structures outside of the angiosperms is uncertain, as is the nature of the carpel itself. We therefore prefer to define it strictly as a structure enclosing the ovules, on which pollen germinates; this eliminates such structures as the seed envelope of *Caytonia*, since pollen has been detected within the micropyles of in situ *Caytonia* ovules.

66. SEEDS: absent (0); radiospermic (1); platyspermic (2); nonadditive.

This character is commonly and widely used in seed plant analyses and phylogenetic discussions; we note that it is exceedingly difficult to score in numerous taxa, particularly some fossils, but differences of opinion also exist for major extant groups (e.g., whether the angiosperms have radiospermic or platyspermic seeds). In fact, the concept of radiospermy versus platyspermy is in itself not well established or clear. For example, "platyspermy" can arise simply by compression of developing ovules by subtending structures. We feel that the character needs to be more clearly defined on the basis of seed structure, instead of shape; shape also changes, sometimes radically, during seed development, and this information is rarely available and even then is not known for the majority of fossil taxa. For extant taxa, we have used the internal arrangement of vascular bundles, and the early stages of development of ovules, when known.

Gnetopsids are scored as radiospermic because the ovules are morphologically, anatomically, and developmentally radiospermic. What appears to be a platyspermic condition in *Welwitschia* is the result of enclosing bracteoles that become flattened and winglike, and not because of a flattened ovule. *Cycas* is scored as polymorphic, based upon evidence presented in Stevenson (1990), but the radiospermic condition in this genus is still unresolved. Although the angiosperms in our analyses are scored as platyspermic, it is not clear whether the concept is applicable without ontogenetic studies across the spectrum of angiosperms.

67. OVULE POSITION: stalked (0); foliar (1); peltate/enclosed (2); nonadditive.

The angiosperms are scored as ambiguous for this character because of the homology of the carpel/placenta. Carpels may be simple leaf-homologues bearing seeds or may be compound structures that include a leaf homologue that subtends an axillary structure bearing seeds (much like a conifer bract/scale complex). It is interesting to note that both groups commonly referred to as sister taxa or outgroups of angiosperms (cycadeoids and gnetopsids) have ovules borne on stalks with no indication of foliar attachment; gnetopsids bear subtending bracts, and at least one interpretation of the sterile scales of cycadeoids is that these are bracts subtending ovules. Thus, a complex origin of the carpel from a leaf homologue/axillary stem seems likely based on outgroup comparison, extending all the way to the coniferophytes and *Ginkgo*.

The peltate/enclosed ovule position is found in the Mesozoic seedfern taxa, which have peltate or laminar/peltate structures that sometimes enfold the ovules. These structures are difficult to interpret as to whether they include both the lamina and axis. We hesitate to score these as homologous with angiosperm carpels for reasons outlined above.

68. OVULE NUMBER: 1–2 (0); many (1).

This character has been widely used in previous analyses in similar forms. Undoubtedly, the problem of foliar versus axial ovules makes it unlikely that such characters are homologous over all seed plants.

69. OVULES: orthotropous (0); anatropous (1).

This character has been used previously, but in our opinion has been improperly coded on the basis of phylogenetic hypotheses instead of on observed morphology in real taxa. We base our definitions of orthotropous and anatropous on the position of the funiculus (ovule stalk) of individual ovules, without assuming that associated structures or groups of ovules later become parts of solitary ovules. The two states are thus a straight ovule in line with the funiculus (orthotropous) or recurved ovule along the funiculus (anatropous). Thus, unlike Doyle & Donoghue (1986a, b, 1987, 1992), we have scored *Caytonia* as having orthotropous ovules. It is the structure that encloses the numerous ovules that is recurved in *Caytonia* (see discussion in fossil section).

70. MICROPYLE: normal (0); tubular (1).

The "normal" micropyle in this case refers to the case in which the inner integument is not elongated into a tube. This character bears further investigation within angiosperms, some of which have extended inner integuments that act as obturators.

71. MICROPYLE ORIENTATION: distal (0); proximal (1).

This character refers to the direction in which the ovule and micropyle point relative to the structure that bears the ovuliferous structure (e.g., axis of the strobilus). It is most useful for differentiating cycad and conifer reproductive structures (Crane, 1988; Stevenson, 1990).

72. OVULE GROWTH: pachychalazal (0); endochalazal (1).

Two contrasting states of ovule growth, pachychalazal and endochalazal, were introduced by Takaso & Bouman (1986). Because this character requires some knowledge of ovule development, it is only applicable at this time to extant groups. The character distinguishes those ovules that have a massive chalaza with integuments generally attached above the middle of the ovule. This is brought about because of unequal development of the chalaza and the integument in such a way as to give rise to a greater part of the seed from the chalazal end in pachychalazal ovules (Takaso & Bouman, 1986). In contrast, gnetopsids and angiosperms appear to have more of an integumentary development (the area above the integument attachment) and are termed endochalazal by Takaso & Bouman (1986). This latter term seems somewhat of a misnomer as the development does not truly occur within the chalazal portion.

73. OUTER SEED ENVELOPE: absent (0); present (1).

We have attempted to develop a character for various layers and/or appendages that envelop the ovule/seed that is less dependent on phylogenetic hypotheses in interpreting and encoding character states than in previous analyses. We thus define outer seed envelope as a layer that directly invests an individual ovule, in contact with the integument ("inner integument") and extending to the micropylar region. We are not convinced of the direct homology or lack of homology of various of these structures, but see no other way to encode such characters that does not bias the results toward particular interpretations. Thus, we have scored as equivalent the second integument of certain angiosperm ovules, the bracteoles of the gnetopsids, and other similar structures in fossil taxa. We have not included arils that are not completely enveloping, such as in the Taxaceae. It also does not include the collar of *Ginkgo* because the nature of that structure does not contribute to the micropylar region and is not understood, even after thorough developmental studies (Takaso, 1980). Although the dual vasculature of the cycad ovule has been interpreted as indicating the dual nature of the cycad "integument" (Stopes, 1905; Stevenson, 1990), because the duality is not present developmentally or in mature ovules, we have scored it as absent.

74. OUTER SEED ENVELOPE: simple (0); bi-parted (1).

Character 76 (outer seed envelope) treats the outer seed envelope when present as either simple or bifid. The bifid condition of the gnetopsids is the result of two opposite bracteoles that are fused, as demonstrated ontogenetically by Martens (1971), Takaso (1984, 1985), and Takaso & Bouman (1986).

75. MEGASPORANGIUM: w/lagenostome (0); w/pollen chamber (1); angiospermous (2); nonadditive.

This character deals with the structure of the apex (micropylar region) of the ovule, and whether the innermost (or sole) integument forms a pollen chamber. The angiospermous type lacks a pollen chamber per se.

76. INNER INTEGUMENT: not-bifid (0); bifid (1).

This character has not been used in previous seed plant analyses, but was clearly illustrated in numerous extant taxa by various workers. The bifid nature of the integument is obvious in mature ovules of certain fossil taxa but only observable during seed development in most extant gymnosperms; this may bias scores against finding bifid seeds in the fossil record. The bifid nature of the integument has been demonstrated for *Ginkgo* (Takaso, 1980) and most conifer genera (Bierhorst, 1971; Takaso, 1981; Takaso & Tomlinson, 1989a, b, 1990, 1991, 1992a, b). There is no evidence for a bifid integument in the gnetopsids (Martens, 1871; Takaso, 1984, 1985; Takaso & Bouman 1986) or angiosperms (Bouman, 1984).

77. CONE SCALE SEED WING: absent (0); present (1).

This character is included to encourage resolution within the conifers.

78. SEED COAT: simple (0); sclerotesta/sarcotesta (1).

The nature of the mature integument has been used in previous analyses in similar form. The simple seed coat has only a sclerified layer in contrast to seeds with distinct fleshy and sclerified layers.

79. INTEGUMENT VASCULATURE: single (0); double (1).

This character refers to the dual vascular system found in the seeds of medullosans and cycads (Stopes, 1905; Crane, 1988; Stevenson, 1990). The origin of this dual vasculature is believed by Stopes (1905) to have been derived from fusion of an outer seed envelope to the integument.

80. SEED CORONULA: absent (0); present (1).

The seed coronula refers to the specialized area of sclerotesta of the seed coat at the micropylar end. This is restricted to the cycad families Stangeriaceae and Zamiaceae (Stevenson, 1990).

81. NUCELLAR CUTICLE: thin (0); thick (1).

Routinely used in analyses of seed plants and the states for taxa are given in most morphology and paleobotany texts.

82. MEGASPORE TETRAD: tetrahedral (0); linear (1); isobilateral (2); nonadditive.

This character is routinely used in analyses of seed plants, and the states for taxa are given in most morphology and paleobotany texts.

83. MEGASPORE WALL: thick (0); thin/absent (1).

Widely used in previous seed plant analyses.

84. MEGAGAMETOPHYTE: monosporic (0); tetrasporic (1).

Widely used in seed plant analyses. Most fossil taxa are problematic and scored as unknown.

85. MEGAGAMETOPHYTE: alveolar (0); nonalveolar (1).

Not previously used in seed plant analyses. Data concerning the alveolar nature of the megagametophyte for extant gymnosperms are from Singh (1978) and Taylor & Taylor (1993); for some fossil taxa, data are from examination of additional published figures. Fortunately, the developmental pattern of the alveolar megagameto-

phyte is observable in mature seeds and thus is preserved in many fossils.

86. ARCHEGONIA: present (0); absent (1).

Widely used in seed plant analyses. Equivocal in many fossils due to inadequate detail of preservation.

87. EGG: cellular (0); free-nuclear (1).

Not previously used in seed plant analyses. This character is observable in mature seeds, and thus scoring is not limited to extant taxa but is also possible in those fossil taxa where archegonia have been observed (e.g., Glossopteris, Cordaites).

88. EARLY EMBRYOGENY: free-nuclear (0); cellular (1).

Data from Singh (1978) and Bierhorst (1971). Unfortunately, this character can only be scored for extant taxa because early embryo stages typically are not preserved in fossils.

89. EMBRYO MATURITY: postshed (0); preshed (1).

Not previously used in seed plant analyses. The states, postshed versus preshed, refer to the timing of embryo development. In preshed maturity, the embryo is well developed before the seed is shed from its parent plant, in contrast to postshed maturity, where the embryo development (and in some instances fertilization) occur after the seed is shed from its parent plant, as in cycads and *Ginkgo*. This character has been scored for some fossils, particularly those that have seeds with well-developed embryos known such as in *Cordaites*. In other cases, where dispersed seeds are known without embryos but well-developed megagametophytes and archegonia are present, we have inferred that embryo maturity is postshed, by analogy with living taxa such as cycads and *Ginkgo*.

90. EMBRYO FEEDER: absent (0); present (1).

This character is scored only for extant taxa and is known only in gnetopsids.

91. SEED GERMINATION: cryptocotylar (0); phanerocotylar (1).

This character is identical to that used by Loconte & Stevenson (1990). In general, cryptocotylar is equivalent to hypogeal and phanerocotylar is equivalent to epigeal germination. This character has been scored as ambiguous for fossil taxa.

92. FLORAL CUP: absent (0); present (1).

The floral cup, as a concave, usually fleshy structure bearing free appendages such as bracts (or perianth) and stamens, staminodes, and possibly carpels, is found in several magnoliid taxa such as *Calycanthus*, various Laurales, and *Eupomatia*, and may have much wider occurrence in modified form than is generally appreciated (e.g., postfertilization structures in Lauraceae). We distinguish between such apparently axial structures and the "calyx cup" of various hamamelidid, rosid, and asterid taxa, in which the contribution of the stem receptacle is either not apparent or is secondary. We have avoided use of the term "hypanthium" because it has been variously and inconsistently applied to structures formed mostly of stem receptacle or mostly of calyx and other floral appendages.

93. CALYX CUP: absent (0); present (1).

See previous character (92) for discussion.

94. PERIANTH: indeterminant/spiral (0); determinant/cyclical (1).

This character is scored as ambiguous for those taxa without perianth.

95. TRIMEROUS ANDROECIUM: absent (0); present (1).

This character is coded as present when one or more cycles of the androecium are in threes or even multiples thereof.

96. STAMEN FORM: filamentous (0); laminar (1).

This character is the traditional distinction between fleshy, laminar stamens and thinner, terete filamentous stamens.

97. STAMEN CONNECTIVE: absent (0); well developed (1).

The occurrence of a well-developed stamen connective, sometimes modified in various manners, is typical of many of the taxa to be considered basal in the angiosperms (Cronquist, 1981).

98. CARPEL ARRANGEMENT: spiral (0); whorled/opposite (1).

Flowers with single carpels have been coded as inapplicable for this character. Data from standard taxonomic texts and herbarium observation.

99. CARPEL NUMBER: 1 (0); 2 (1); 3 (2); 4/5 (3); nonadditive.

Scored only for those taxa with stabilized numbers of carpels (character 100).

100. CARPEL NUMBER: indeterminant (0); determinant (1).

Indeterminant carpel refers to spirals or whorls that are not fixed on particular modal numbers.

101. OVARY: apocarpous (0); syncarpous (1); syncarpous-inferior (2); additive.

This character is treated as additive because syncarpy is a prerequisite for an inferior ovary (in the sense used here). Taxa such as *Calycanthus* have an apocarpous gynoecium but are perigynous and are scored as having a floral cup, not a syncarpous inferior ovary. In all taxa in our analyses scored as syncarpous-inferior, the calyx and or other floral appendages are clearly adnate to a syncarpous ovary.

102. PLACENTATION: marginal laminar (0); apical (1); basal (2); nonadditive.

This character is not related to number of ovules; thus, two ovules may be apical or marginal, but in the taxa we included, taxa with numerous ovules were always state 0. This would not be the case if more angiosperm taxa were included.

FUNCTIONAL CONSTRAINTS AND *rbc*L EVIDENCE FOR LAND PLANT PHYLOGENY[1]

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ABSTRACT

Although the proportion of "functional" DNA in eukaryotic genomes is both debatable and subject to definition, most sequences gathered for phylogenetic purposes are indisputably functional. For example, patterns of variation are likely to be strongly constrained in ribosomal RNAs because of their structural and catalytic roles in protein translation, and in protein-coding genes, because of protein function itself. Although seemingly obvious, these concerns are usually ignored by workers producing gene trees. We have examined the extent of functional constraints in land-plant *rbc*L sequences. Not only do *rbc*L sequences appear to change with essentially clocklike regularity, but nucleotide-based cladograms imply that approximately 97.5% of codon changes on internal branches are functionally neutral (i.e., synonymous or functionally labile). From this perspective, *rbc*L evolution appears to be strongly constrained by function. Transforming nucleotide data into ad hoc string recognitions alters the size of the unit character sufficiently to highlight "blocks" of conservative information that may or may not be functionally constrained. Simultaneous cladistic analysis of all available evidence will highlight the proportion of congruent information, despite diverse functional constraints among the characters analyzed. We demonstrate the strength of this approach using different forms of the same *rbc*L evidence (i.e., nucleotides, strings, or amino acids) in combination with the seed-plant data of Nixon et al.

Diversification of the major clades of extant land plants probably dates from the Silurian to Cretaceous. During the Silurian–Devonian, liverworts, hornworts, mosses, and tracheophytes formed distinct lineages. Differentiation of the tracheophyte clades, notably angiosperms and other seed plants, began by the Devonian. The estimation of land-plant phylogeny, a research goal spanning over 400 million years of cladogenesis and extinction, is no simple task. For example, many groups lack strong morphological similarities that might suggest patterns of relationship.

Recent years have seen an explosion of interest in molecular information, with its promise of easily interpreted similarities for bridging otherwise large phenotypic gaps. In particular, the plastid *rbc*L gene (which encodes the large subunit of RuBisCO: ribulose-1,5-bisphosphate carboxylase/oxygenase, a primary enzyme in carbon fixation) has been sequenced extensively, with primary emphasis on the angiosperms (Clegg, 1993; Chase et al., 1993). Arguing from expected synonymous substitutions per site under a particular rate assumption, Clegg (1993) suggested that *rbc*L sequences should be phylogenetically informative for the time interval 400–100 million years before present. We argue here that this and similar assertions are incomplete. From direct estimation of *total* substitutions (as optimized on cladograms; see Albert et al., 1992a, 1993; Albert & Mishler, 1992 Albert et al., 1993)

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we will demonstrate that divergence-time asymmetries among taxa restrict *rbc*L-based hypotheses of land-plant phylogeny far more than do rate asymmetries.

We have examined the internal stability of land-plant *rbc*L evidence through conversion of nucleotide information into different data forms, including presence/absence of ad hoc nucleotide strings. Cladograms produced from nucleotide, string, and translated amino acid data are only partially congruent. Character optimization on both nucleotide and string trees reveals extensive functional conservation through the predominance of silent changes and labile (function-conserving) amino acid replacements. Hence, *rbc*L nucleotides are no less functionally constrained than morphological characters (contra Olmstead, 1989; Sytsma et al., 1991; Clegg, 1993).

Although the separation of protein-functional from cladogenetic history may not be entirely possible, the extent to which functional history reflects phylogeny might be assessed through congruence studies with characters expected to carry diverse patterns of functional constraints. As such, we have performed total-evidence analyses at the seed-plant level using, as a "constant," a new matrix of primarily morphological data (Nixon et al., 1994, this issue). It emerges that combination of *rbc*L nucleotide, amino acid, or string data with this matrix produces highly compatible cladistic hypotheses. These studies point to (i) the commonality of information in different data forms representing the same evidence, and (ii) the power of simultaneous evaluation of all available evidence and weakness of further production of *rbc*L gene trees (cf. Kluge, 1989; Barrett et al., 1991; Donoghue & Sanderson, 1992; Jones et al., 1993; Mishler, 1994).

The Rate "Problem"

As has been pointed out in several recent papers, sequence change in the *rbc*L gene is not strictly clocklike (Albert et al., 1992a; Bousquet et al., 1992; Gaut et al., 1992; Clegg, 1993). Here, we provide a number of new comparisons (Table 1) based on patristic distances between woody taxon pairs from Search II of Chase et al. (1993). It is clear that our own estimates and those of other workers all fall within a very narrow range of absolutely low values. The mean rate per taxon pair investigated here is approximately 2×10^{-10} total substitutions per site per million years; Wendel & Albert (1992) estimated $5–7 \times 10^{-10}$ for three herbaceous-pair comparisons. Lineage-specific rate differences were found by Bousquet et al. (1992) and in the relative-rate tests of Gaut et al. (1992), but absolute rate estimates do not differ substantially from our own findings. Thus, whereas *rbc*L data cannot be considered perfectly ultrametric (i.e., satisfying a clock assumption), the small range of absolute variation suggests that some predictions of the clock hypothesis still apply. For example, the relationship between time and the accumulation of nucleotide substitutions may be nearly linear. We term this condition, apparently characterizing *rbc*L sequence data, "quasi-ultrametric."

Quasi-ultrametricity has several important implications. One is that the extent of sequence divergence in a given taxon sampling should roughly reflect the timing of underlying cladogenetic events. If all such events are ancient, extensive sequence differences among all taxa are to be expected (Fig. 1; cf. Donoghue & Sanderson, 1992, fig. 15.3). If some cladogenetic events are ancient whereas others are much more recent, expected sequence divergence in a data set would be prominently skewed (Fig. 2). As these properties become extreme, parsimony analysis will be hampered by the increased probability of parallel changes among either anciently diverged or divergence-time-asymmetric sequences (Figs. 1, 2; cf. Donoghue & Sanderson, 1992: 347–349). Given that A, T, G, and C are the only character-state alternatives, either scenario is likely to produce patterns of similarity that may be nonhomologous and therefore cladograms that are ahistorical. This is precisely the "long branches attract" issue raised by Felsenstein (1978) and others.

Although asymmetrical rates of sequence change are often invoked to explain branch attraction behavior (see Clegg and Zurawski, 1992: 10, with reference to *rbc*L), the problem is better defined in terms of both rate and divergence time as their product, per-character change: the λ of Albert et al. (1992a, 1993; Albert & Mishler, 1992; cf. Hendy & Penny, 1989). With quasi-ultrametric data, rate asymmetry is unimportant in this regard; time through which a branch exists becomes the central factor. As such, our expectation of the performance of parsimony analysis on *rbc*L data must include our ability to estimate both the absolute and relative timing of cladogenetic events inherent to particular data matrices. Of course, this may not always be possible.

An additional implication of quasi-ultrametricity is the near satisfaction of selective neutrality. A molecular clock is predicted by the neutral theory of molecular evolution; equal rates of mutation and fixation are the expectation (see Kimura, 1983;

TABLE 1. "Phylogenetic" estimation of total substitution rate for 19 woody-taxon pairs. The rate of sequence divergence was calculated as per-site divergence (the patristic distance, D_p, divided by the number of nucleotides compared) divided by time since cladogenesis (Albert et al., 1992a). Average rates for individual taxa are half of the values shown. Data are from Search II of Chase et al. (1993); systematic error associated with that analysis can be expected to affect all calculations equally. Divergence time assumptions are based upon geologic dates associated with vicariant disjunctions (with the exception of all Arecaceae comparisons, which follow from the arguments of Wilson et al., 1990).

Taxon pair	Area	Divergence time assumption	D_p	Divergence rate (subst./site· taxon pair)
Callitris rhomboidea R. Br. ex Rich. *Widdringtonia cedarbergensis* Marsh (Cupressaceae)	Australia Africa	100 My[a]	55	3.85×10^{-10}
Metasequoia glyptostroboides Hu & W. C. Chang *Sequoiadendron giganteum* (Lindl.) J. Buchholz (Taxodiaceae)	Asia N. America	40 My[b]	16	2.80×10^{-10}
Illicium parviflorum Michx. ex Vent *Austrobaileya scandens* C. T. White (Illiciaceae/Austrobaileyaceae)	N. America/Asia Australia	200 My[c]	54	1.89×10^{-10}
Drimys winteri J. R. & G. Forst. *Belliolum* sp. (Winteraceae)	S. America New Caledonia	100 My	21	1.47×10^{-10}
Drimys winteri J. R. & G. Forst. *Tasmannia insipida* DC. (Winteraceae)	S. America Tasmania	100 My	14	0.98×10^{-10}
Canella winteriana (L.) Gaertn. *Belliolum* sp. (Canellaceae/Winteraceae)	N. America New Caledonia	200 My	78	2.73×10^{-10}
Canella winteriana (L.) Gaertn. *Tasmannia insipida* DC. (Canellaceae/Winteraceae)	N. America Tasmania	200 My	67	2.35×10^{-10}
Liriodendron tulipifera L. *Liriodendron chinense* (Hemsl.) Sarg. (Magnoliaceae)	N. America Asia	40 My	10	1.75×10^{-10}
Calycanthus chinensis Cheng & S. T. Chang *Idiospermum australiense* (Diels) S. T. Blake (Calycanthaceae/Idiospermaceae)	Asia N. America Australia	200 My	28	0.98×10^{-10}
Chimonanthus praecox (L.) Link *Idiospermum australiense* (Diels) S. T. Blake (Calycanthaceae/Idiospermaceae)	Asia Australia	200 My	24	0.84×10^{-10}
Chamaedorea costaricana Oerst. *Drymophloeus subdistichus* (H. E. Moore) H. E. Moore (Arecaceae)	Americas S. Pacific	60 My[d]	15	1.75×10^{-10}
Chamaedorea costaricana Oerst. *Vypa fruticans* Wurb. (Arecaceae)	Americas S. Pacific/India	60 My	20	2.33×10^{-10}
Serenoa repens (Bartram) Small *Drymophloeus subdistichus* (H. E. Moore) H. E. Moore (Arecaceae)	Americas S. Pacific	60 My	18	2.10×10^{-10}

TABLE 1. Continued.

Taxon pair	Area	Divergence time assumption	D_p	Divergence rate (subst./site·taxon pair)
Serenoa repens (Bartram) Small *Nypa fruticans* Wurb. (Arecaceae)	Americas S. Pacific, India	60 My	23	2.68×10^{-10}
Betula nigra L. *Casuarina litorea* L. (Betulaceae/Casuarinaceae)	N. Hemisphere Australia	200 My	35	1.23×10^{-10}
Nothofagus dombeyi (Mirb.) Oerst. *Nothofagus balansae* (Baill.) Steenis (Nothofagaceae)	S. America New Caledonia	100 My	30	2.10×10^{-10}
Galphimia gracilis Bartl. *Acridocarpus natalitius* A. Juss. (Malpighiaceae)	S.-N. America[a] Africa Madagascar New Caledonia	100 My	34	2.38×10^{-10}
Bucella nucifera Chodat *Acridocarpus natalitius* A. Juss. (Malpighiaceae)	S. America Africa/Madagascar/ New Caledonia	100 My	33	2.31×10^{-10}
Mascagnia stannea (Griseb.) Nied. *Acridocarpus natalitius* A. Juss. (Malpighiaceae)	S.-N. America Africa/Madagascar/ New Caledonia	100 My	34	2.38×10^{-10}
Range				3.01×10^{-10}
Mean				2.05×10^{-10}
S.D.				$\pm 0.75 \times 10^{-10}$

Standard time figure used to represent the breakup of Gondwana (rounded to the nearest 100 My (million years) from 130 My, as estimated using Terra Mobilis® 2.1 by C. R. Denham and C. R. Scotese; see Wendel & Albert, 1992: 137).

Standard time figure (ca. early Oligocene) used to represent disruption of the boreotropical interchange between North America and Eurasia (see Lavin & Luckow, 1993).

Standard time figure used to represent separation of the Northern and Southern Hemispheres upon the breakup of Pangaea (rounded to the nearest 100 My from 160 My, as estimated using Terra Mobilis® 2.1 by C. R. Denham and C. R. Scotese; see Wendel & Albert, 1992: 137).

[a] Divergence date used by Wilson et al. (1990), based on the fossil record.

North American Malpighiaceae are here interpreted as representing range expansion from South America.

Nei, 1987). Quasi-ultrametric data may imply selection coefficients very close to neutrality. Remembering that the underlying premise of selective neutrality is the neutral effect of point mutations, nearly clocklike sequence evolution should involve a large proportion of such changes, fixed as effectively neutral substitutions. Such substitutions would be expected to be mainly silent (i.e., synonymous with respect to amino acid[8]), and, with regard to amino acid replacements, functionally conservative (labile). Quasi-ultrametricity in *rbc*L nucleotide sequences is thus an expected manifestation of strong constraints on protein function.[9]

UNIT CHARACTERS AND FUNCTIONAL CONSTRAINTS

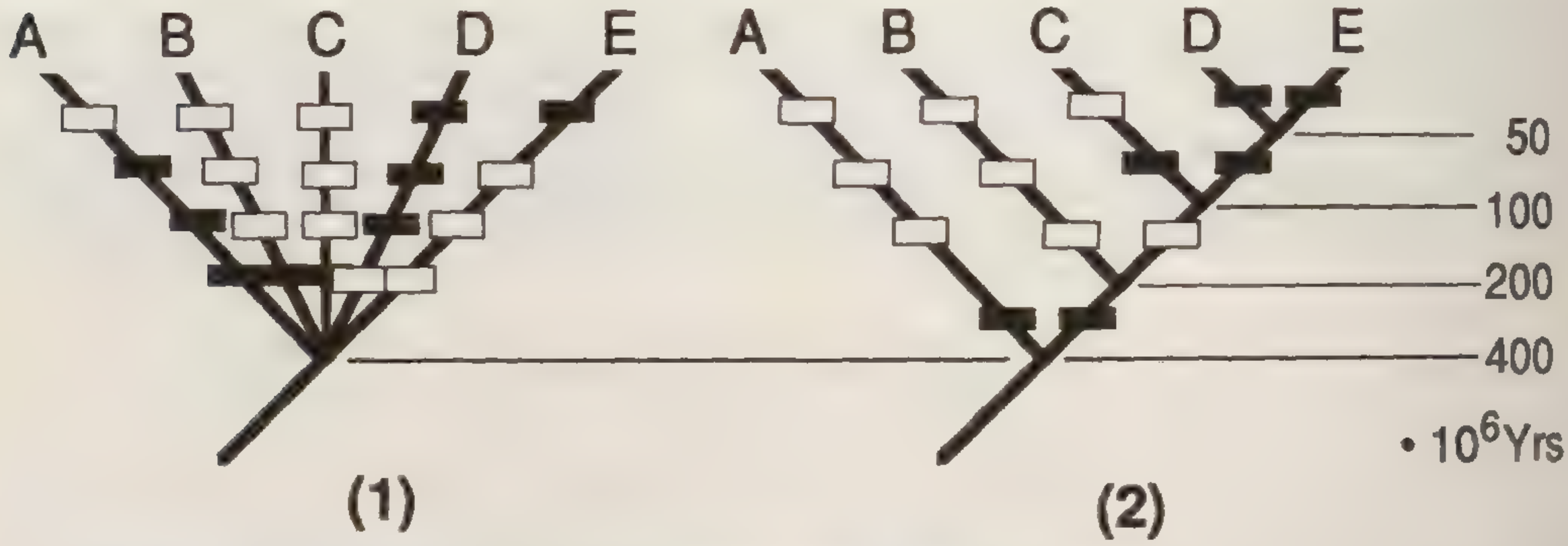
As recently reviewed by Clegg (1993), a number of systematic and evolutionary studies have relied solely on *rbc*L sequence variation. Such analyses make the implicit assumption that *rbc*L nucleotides are independent and potentially informative markers of cladogenetic events. As discussed above with respect to total rates of change, if all branching events under consideration are relatively recent, parsimony analysis may be expected to proceed with a reduced probability of spurious branch attraction because of the absolutely lower expected

[8] See Clegg (1993) on synonymous rates for *rbc*L; note that only *total* substitution rates are relevant to cladistic methods because all informative variation is considered.

[9] Assuming that purifying selection eliminates mutations deleterious to protein function and that f is the fraction of such mutations, the neutral theory may be reformulated as

$$S = (1 - f)\mu$$

where S is the total substitution rate per site and μ is the mutation rate (after Nei, 1987: 52, 411).



FIGURES 1 AND 2. Patterns of historical versus spurious similarity resulting from symmetrically ancient and asymmetrical time-samples. In both cases, time-sample refers to the nodes on these imaginary trees. In (1), all nodes are essentially time-coincident at 400 My, so the "true tree" appears polytomous. In (2), the cladogenetic events indicated occur asymmetrically with respect to time, ranging from 400 to 50 My since divergence. Possible patterns of nucleotide change are indicated by the filled and open rectangles; the former represent unadulterated markers of cladogenetic history, whereas the latter represent spurious character-state similarity resulting, e.g., from multiple nucleotide substitutions. In (1), these patterns of similarity are approximately equal in extent (because of nearly clocklike substitutional behavior) but are in partial conflict with each other; parsimony analysis may include resolutions containing some proportion of ahistorical evidence or even alternatives comprising totally spurious patterns. This might be the expectation if taxa A through E were, e.g., *Isoetes*, *Selaginella*, *Psilotum*, *Equisetum*, and *Angiopteris*. In (2), which approximates the situation in simultaneous studies of sporing and seed plants, the problems of (1) are only partially alleviated. Patterns of convergent similarity between the oldest taxa, A and B, will result in most parsimonious reconstructions that pair these taxa spuriously. As divergence time becomes shallower, the reduced likelihood of multiple changes at sites will insure that D and E are paired historically. Although C is linked with (D, E) by "true" similarity, this relationship may be broken by false similarities between B and C as well as between B, (C, D, E). In summary, comparing only anciently diverged lineages with *rbc*L may suggest patterns of relationship that represent a hopelessly even mixture of historically reliable and nonreliable similarity. Likewise, comparison of ancient and recently diverged clades may have the same problem near the base while being relatively more consistent near the tips. This condition may characterize the *rbc*L-based results shown in this paper.

sequence divergence and relatively lower associated likelihood of character-state parallelism. This "time-sampling" strategy has been employed in circumscribed studies ranging from particular angiosperm groups (e.g., Conti et al., 1993; Kron & Chase, 1993; Rodman et al., 1993) to seed plants as a whole (Chase et al., 1993). Here, a "time sample" refers to the nodes rather than the terminals on an imaginary tree; as such, a time sampling is the collection of absolute and relative timings of underlying cladogenetic events in a data matrix. Of course, the nodes of a cladogram are not discernible a priori to analysis, but their absolute and relative timing may be estimated by external criteria (e.g., the fossil record; cf. Norell & Novacek, 1992).

Initial attempts to analyze time samples beyond angiosperms and other seed plants (i.e., including *rbc*L sequences from sporing plants; Albert et al., 1992b) resulted in cladistic patterns familiar from studies based on ribosomal DNA (rDNA) variation (e.g., monophyletic gymnosperms or combinations of gymnosperm lineages, a seed-plant "root" at the Gnetales, an angiosperm "root" at the monocots; see Troitsky et al., 1991; Zimmer et al., 1989; Hamby & Zimmer, 1992). These results, however, are in conflict with cladistic studies based on morphological characters (see below). Ribosomal RNAs, with their structural and catalytic roles in protein translation, are obviously under enormous functional constraints. Like *rbc*L, rDNAs may also exhibit nearly clocklike substitutional behavior in those positions that are "free" to vary. If the absolute rates of change approximate the low values estimated for *rbc*L, analysis of corresponding time samples might be expected to result in corresponding patterns of homologous and parallel similarity, and therefore similar hierarchial reconstructions (cf. Donoghue & Sanderson, 1992: 347–349).

To gain insight into the topological effects of vastly asymmetrical time samples (see Fig. 2), we have combined *rbc*L information from "bryophytes," "pteridophytes," "gymnosperms," and angiosperms (Table 2). If the substitutional process is effectively clocklike among these taxa, some effects of functional constraints in land-plant *rbc*L evolution should be discernible (as may be spurious branch attractions; see The Rate "Problem," above); we explore this cladistically from both the primary nucleotide data as well as ad hoc nucleotide strings. The *rbc*L data are examined also at the

TABLE 2. *rbc*L sequences used for data transformation and cladistic analysis. These are listed by taxon and by GenBank accession number and/or literature reference where sequence data first appeared. Voucher information, where available, is given by these sources.

Taxon	GenBank accession or literature reference
Conocephalum conicum (L.) Lindb.	Mishler et al., 1994
Lophocolea heterophylla (Schrad.) Dumort.	Mishler et al., 1994
Anthoceros punctatus L.	Mishler et al., 1994
Andreaeobryum macrosporum Steere & B. Murray	Mishler et al., 1994
Ophioglossum engelmannii Prantl	L11058 (J. R. Manhart, in press)
Psilotum nudum (L.) P. Beauv.	L11059 (J. R. Manhart, in press)
Isoetes melanopoda J. Gay & Durieu	L11054 (J. R. Manhart, in press)
Lycopodium digitatum A. Br.	L11055 (J. R. Manhart, in press)
Angiopteris evecta (G. Forst.) Hoffm.	L11052 (J. R. Manhart, in press)
Equisetum arvense L.	L11053 (J. R. Manhart, in press)
Selaginella sp.	L11280 (J. R. Manhart, in press)
Botrychium biternatum (Sav.) Underwood	L13474 (J. R. Manhart, in press)
Taxus × *media*	Chase et al., 1993
Taxodium distichum (L.) Rich.	Soltis et al., 1992
Podocarpus gracilior Pilg.	X58135 (Bousquet et al., 1992)
Ginkgo biloba L.	Chase et al., 1993
Cycas revoluta L.	B. Schutzman, *s.n.*, FLAS, (M. W. Chase, unpublished)
Stangeria eriopus (Kunze) Baill.	Chase et al., 1993
Zamia inermis Vovides, J. D. Reese & M. Vásquez-Torres	L12683 (Chase et al., 1993)
Ephedra tweediana C. A. Mey.	L12677 (Chase et al., 1993)
Welwitschia mirabilis Hook. f.	Chase et al., 1993 (G. R. Furnier)
Gnetum gnemon L.	L12680 (Chase et al., 1993)
Chloranthus japonicus Siebold	L12640 (Chase et al., 1993)
Piper betle L.	L12660 (Chase et al., 1993)
(*Drimys*) *Tasmannia insipida* DC.	L01957 (Albert et al., 1992c)
Calycanthus chinensis Cheng & S. T. Chang	L12635 (Chase et al., 1993)
Eupomatia bennettii F. Muell.	L12644 (Chase et al., 1993)
Magnolia macrophylla L.	Golenberg et al., 1990
Persea americana Mill.	Golenberg et al., 1990
Trochodendron aralioides Siebold & Zucc.	L01958 (Albert et al., 1992c)
Ceratophyllum demersum L.	M77030 (Les et al., 1991) plus nucleotides 1184–1428 from Qiu et al., 1993
Nymphaea odorata Aiton	M77035 (Les et al., 1991) plus nucleotides 1184–1428 from Qiu et al., 1993
Lilium superbum L.	L12682 (Albert et al., 1992a)
Platanus occidentalis L.	L01943 (Albert et al., 1992c)
Caltha palustris L.	L02431 (Albert et al., 1992c)
Dillenia indica L.	L01903 (Albert et al., 1992c)
Chrysolepis (*Castanopsis*) *sempervirens* (Kellogg) Hjelmq.	Chase et al., 1993
Betula nigra L.	L01889 (Albert et al., 1992c)
Casuarina litorea L.	L01893 (Albert et al., 1992c)
Hamamelis mollis Oliv.	L01922 (Albert et al., 1992c)

amino acid level for hierarchic compatibility with the nucleotide and string evidence.

NUCLEOTIDES

The nucleotide is the smallest unit character available in DNA information. With only four states possible at any given site, nucleotide data are subject to parallelism among sequences when the number of changes per site, λ (= rate·time), becomes large. Unlike some morphological characters, nucleotide data are usually analyzed cladistically with no assumed transformation series (i.e., nonadditive steps; Fitch, 1971). For such procedures, Albert et al. (1993) examined the potential for spurious branch attraction under Felsenstein's (1978) simplified four-taxon scenario. State-change probabilities with Jukes-Cantor (Jukes & Cantor, 1969)

and Kimura 2-parameter (Kimura, 1980) corrections for multiple changes at sites were considered in addition to observed changes only because of the prospect of reducing character-state parallelisms. All calculations indicated a very small parameter region under which branch attraction could be expected, provided that λ values remained small (i.e., less than approximately 0.1; see Albert et al., 1992a). For quasi-ultrametric data, differences in λ values must principally result from divergence time differences.

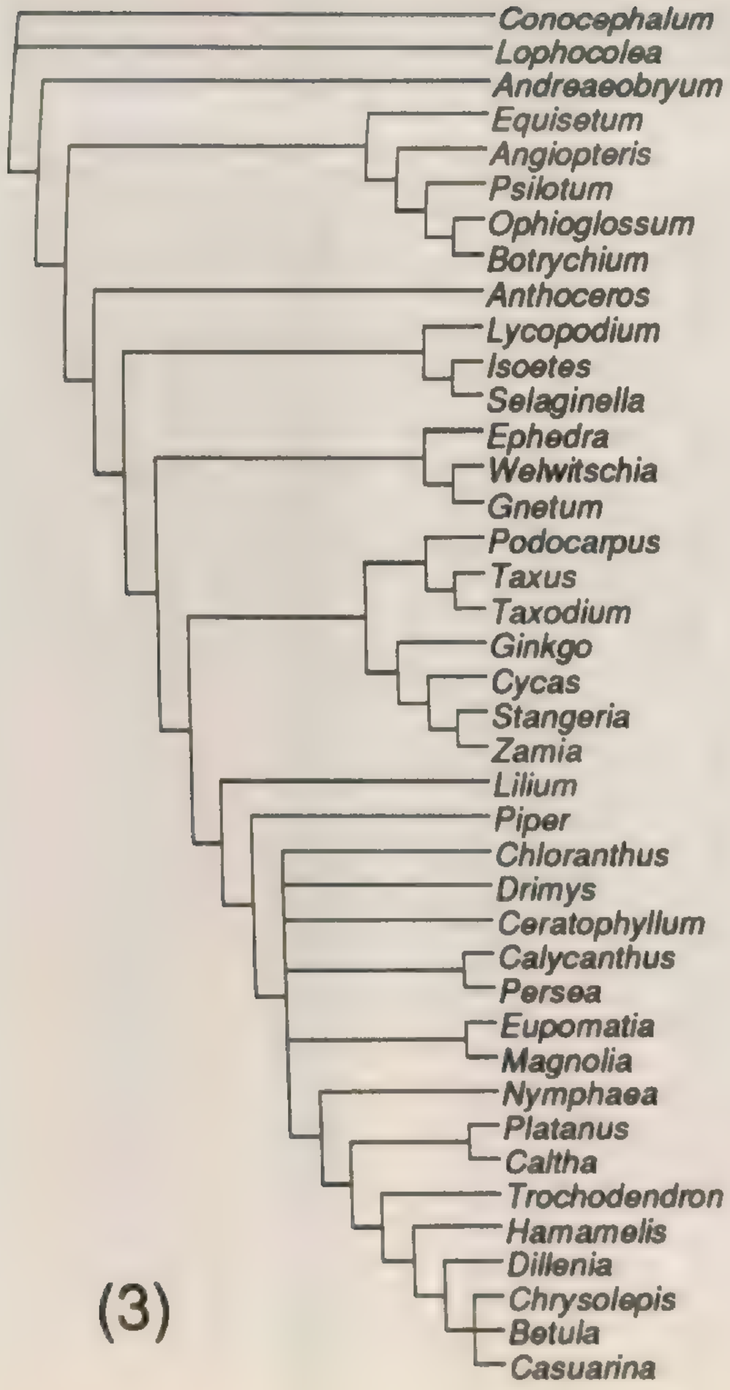
The bryophyte lineages examined here could easily be pre-Silurian; the pteridophytes no later than Devonian; the seed-plants appearing by the Carboniferous; the angiosperms by the Cretaceous, followed by their diversification through the Tertiary—a time range potentially spanning 500–5 million years before present. Thus, even without a priori knowledge of precise divergence times, it is reasonable to approximate upper and lower λ-bounds from this range and our estimates of total sequence divergence. The mean rate for woody taxa (Table 1), averaged for single lineages by halving the divergence value, is approximately 1.0×10^{-10} nucleotide substitutions per site per year. Similarly, the estimates for herbaceous taxa (Wendel & Albert, 1992) range between $2.5–3.5 \times 10^{-10}$. Assuming that bryophytes and pteridophytes fall into the range $1.0–3.5 \times 10^{-10}$ as well, λ values are estimated to lie between 0.05–0.175 (500 My) and 0.0005–0.00175 (5 My). On a four-taxon tree, some combinations of these values would yield spurious branch attractions (see Albert et al., 1993). Here, we are working with 40 taxa and a greater potential for inconsistent results (see Penny et al., 1991).

Data analysis. Nucleotide sequences (unambiguously aligned by sight and excluding the 30 5′-most positions, which incorporated only primer information for some taxa; Table 2) were analyzed with PAUP 3.1.1 (Swofford, 1993) using the Fitch criterion (Fitch, 1971; cf. Albert et al., 1993) with ACCTRAN (accelerated transformation) optimization (Farris, 1970; Swofford & Maddison, 1987). The heuristic search option was used with 100 random replicates of data addition sequence, COLLAPSE, MULPARS, and TBR (tree bisection-reconnection) branch-swapping. The consistency and retention indices (C and R, respectively; Kluge & Farris, 1969; Farris, 1989a) were also calculated. Five hundred fifteen nucleotide positions showed patterns of similarity among taxa.

Eight equally parsimonious cladograms were found ($C = 0.362$ (including all data), $R = 0.523$). The strict and combinable component consensus trees (Bremer, 1990) were identical (see Fig. 3). All trees indicate that (i) hornworts are nested inside the tracheophyte clade, (ii) lycopods rather than ferns plus *Equisetum* represent the sister group to seed plants, (iii) Gnetales represent the sister group of all other seed plants, (iv) conifers, *Ginkgo*, and cycads form the monophyletic sister group to angiosperms, and (v) monocots are basalmost in the angiosperms, followed by *Piper*. Characteristics (iii) and (iv) are shared with the rDNA analysis of Hamby & Zimmer (1992) but not with the morphological analyses of Crane (1985), Doyle & Donoghue (1986, 1992), Loconte & Stevenson (1990), and Nixon et al. (1994). Characteristic (i) is in conflict with both morphological and molecular cladistic studies (Mishler & Churchill, 1985; Mishler et al., 1994, this issue). Characteristic (ii) contrasts both with morphological data (Bremer, 1985) and with the chloroplast genome structural findings of Raubeson & Jansen (1992) that link all tracheophytes except the lycopods, which have the plesiomorphic (i.e., liverwortlike) state. Characteristic (v) contrasts with the results of morphological (Donoghue & Doyle, 1989; Loconte & Stevenson, 1991; Taylor & Hickey, 1992) and some rDNA (Hamby & Zimmer, 1992; cf. Zimmer et al., 1989) analyses.

Function and phylogeny. Needless to say, not all of the above observations can represent the truth about land-plant history. The groups found in the nucleotide-based parsimony analysis (Fig. 3) may well reflect historical reality, but the nature of that reality could be other than strictly phylogenetic. From our argument about nearly clocklike rates and the functional constraints that may produce them, it is reasonable to suppose that some or even all of the branchings depicted in Figure 3 may reflect primarily spurious similarities rather than phylogenetic homologies. We have assessed possible constraints on *rbc*L evolution by examining the amino acid changes implied on the internal

FIGURES 3–5. Combinable component consensus trees summarizing the results of parsimony analyses of *rbc*l evidence as (3) nucleotide, (4) string, and (5) amino acid data. For (3), the strict consensus is identical; for (4) and (5), the single combinable components are indicated by the percentage of most parsimonious trees that resolve what would otherwise be polytomies. Implications of the different topologies are discussed in the text.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Equisetum
Angiopteris
Psilotum
Ophioglossum
Botrychium
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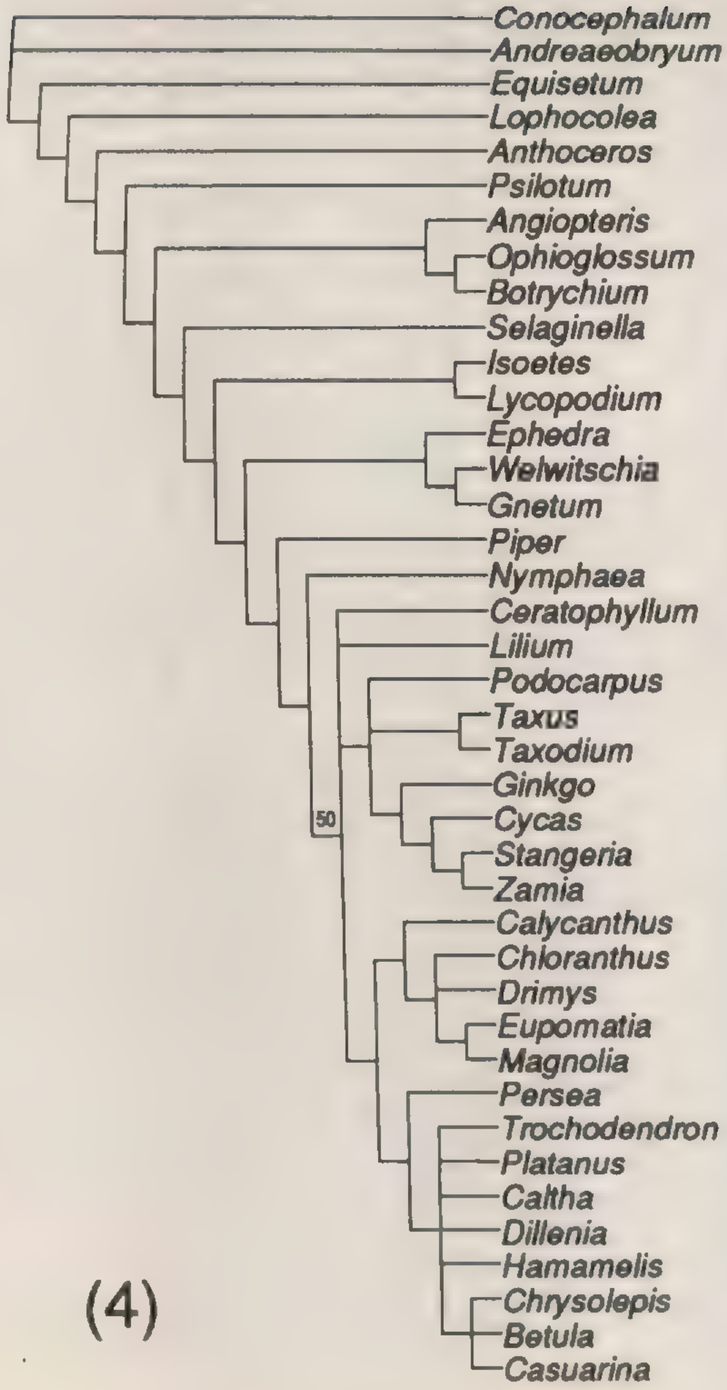
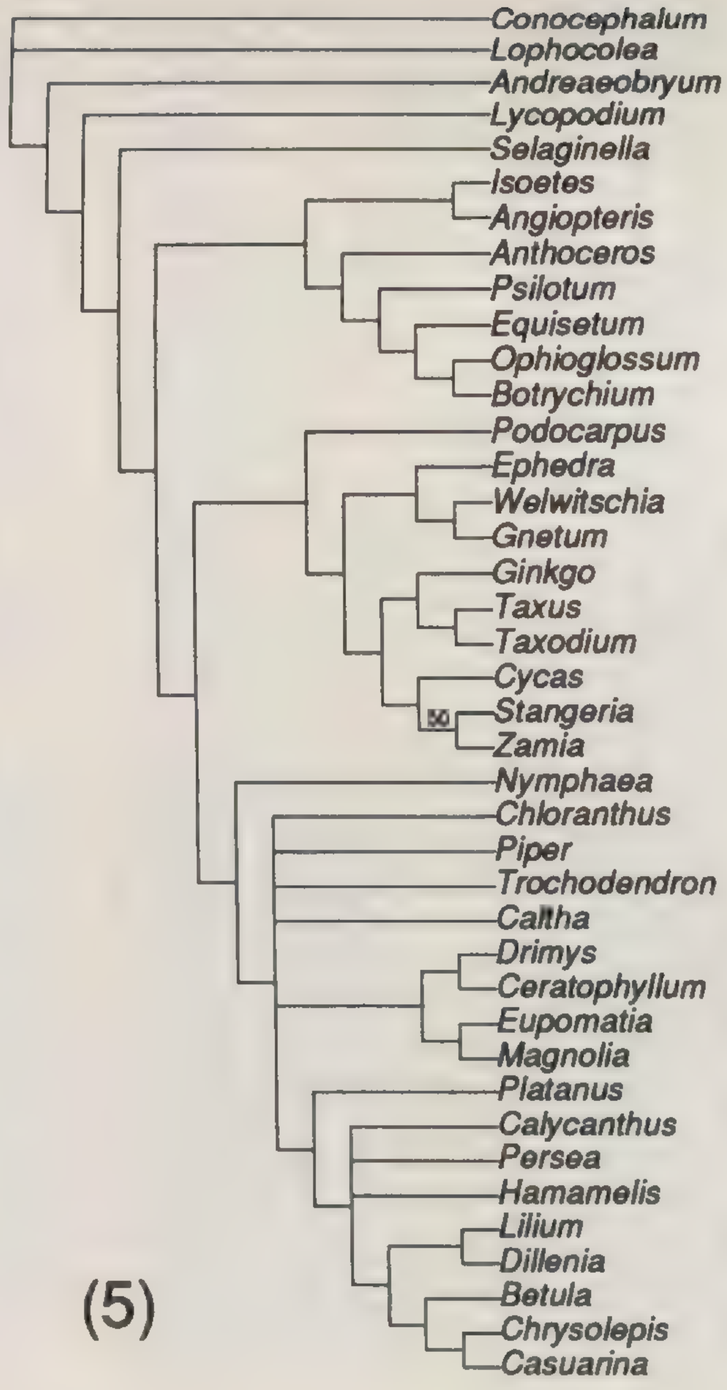
Isoetes
Selaginella
Ephedra
Welwitschia
Gnetum
Podocarpus
Taxus
Taxodium
Ginkgo
Cycas
Stangeria
Zamia
Lilium
Piper
Chloranthus
Drimys
Ceratophyllum
Calycanthus
Persea
Eupomatia
Magnolia
Nymphaea
Platanus
Caltha
Trochodendron
Hamamelis
Dillenia
Chrysolepis
Betula
Casuarina

(3)


Conocephalum
Andreaeobryum
Equisetum
Lophocolea
Anthoceros
Psilotum
Angiopteris
Ophioglossum
Botrychium
Selaginella
Isoetes
Lycopodium
Ephedra
Welwitschia
Gnetum
Piper
Nymphaea
Ceratophyllum
Lilium
Podocarpus
Taxus
Taxodium
Ginkgo
Cycas
Stangeria
Zamia
Calycanthus
Chloranthus
Drimys
Eupomatia
Magnolia
Persea
Trochodendron
Platanus
Caltha
Dillenia
Hamamelis
Chrysolepis
Betula
Casuarina

(4)


Conocephalum
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Botrychium
Podocarpus
Ephedra
Welwitschia
Gnetum
Ginkgo
Taxus
Taxodium
Cycas
Stangeria
Zamia
Nymphaea
Chloranthus
Piper
Trochodendron
Caltha
Drimys
Ceratophyllum
Eupomatia
Magnolia
Platanus
Calycanthus
Persea
Hamamelis
Lilium
Dillenia
Betula
Chrysolepis
Casuarina

(5)

branches of one of the eight equally most-parsimonious trees (Appendix I). As summarized in Table 3, over 84% of the inferred nucleotide substitutions on internal branches are silent with regard to amino acid identity. The percentage of nucleotide changes incurring functionally labile amino acid replacements (judged using the PAM-250 log-odds matrix of Dayhoff et al., 1978: 352; see Table 3) amount to an additional ≈ 13%. Viewed as a whole, 97.5% percent of all synapomorphous nucleotide changes are expected to have little or no effect on protein function. With a maximum of only 2.5% of these changes incurring non-labile amino acid replacements of potential structural/functional distinction (see Table 3), *rbc*L sequences appear heavily burdened by forces leading to functional conservation.[10] Thus, the challenge for land-plant cladistics is to determine how strongly functionally constrained variation may also reflect phylogenetic patterns.

STRINGS

The ideal "unit" character in phylogenetic analysis is one that truly evolves as an independent unit, meaning one that independently undergoes transformations from one condition to another that are hierarchically correlated (i.e., congruent; cf. Farris, 1969) with those of other such characters. For molecular data, this may often be the individual nucleotide, but possibly also a contiguous length of DNA in an insertion/deletion event, several non-contiguous nucleotide positions that are functionally associated (e.g., because of higher order RNA or protein structure), a unique codon for a functionally constrained amino acid, or a whole chromosome in a karyological change. It is of course difficult to assess such possibilities a priori, but it is nonetheless important to begin to develop methods to examine the issue empirically.

We have thus examined some means by which the functional/phylogenetic evidence manifest in a given set of *rbc*L sequences might be represented by data forms other than nucleotide positions and their character states. The nucleotide is indeed the smallest unit character in *rbc*L evidence, but it is not necessarily the most informative nor most consistent. First, nonadditive optimization of multistate characters may restrict potential topological resolution (e.g., a 4-state, nonadditive character can have minimum homoplasy if optimized as three autapomorphies). Additionally, direct analysis of nucleotide sequences from protein-coding genes ignores constraints imposed both by the genetic code and protein function; codon positions may be both intra- and inter-correlated (Fitch & Markowitz, 1970; Fitch, 1986).

A data transformation that may overcome these shortcomings stems from the early comparison of oligonucleotide catalogues (and even whole chromosomes; see Farris, 1978; Fox et al., 1980; Bremer & Bremer, 1989) prior to the DNA sequencing revolution: production of ad hoc nucleotide strings. Our procedure (analogous to generating mapped restriction site data) may be outlined thus: (i) generate strings of random A, T, G, and C content varying randomly in size between 6 and 21 base pairs (so that a minimum and maximum of two and seven codons are included), (ii) scan *rbc*L sequence data for the presence/absence of given strings, (iii) record recognitions by both base position and taxon, (iv) treat multiple positional recognitions by a given search string separately, (v) treat all recognitions found in two or more taxa as binary characters for cladistic analysis (sequences that have missing information at a string position are coded accordingly). Another procedure for producing string data from nucleotide sequences has been developed by J. S. Farris (unpublished); sequences are subdivided into a prespecified number of string characters ("supersites"), each of which is assigned as many states as necessary to explain observed variation. Farris's method guarantees both a complete transformation of the entire sequence as well as the non-overlap of string characters, unlike the approach used here (see below and Appendix II).

The net effect of transforming sequences into strings is twofold: (i) it incorporates more information (in terms of nucleotides or codons spanned) in a larger unit character, and (ii) decreases the probability that independent gains of the same character-state are represented in data matrices (although, in parsimony analyses, binary characters are more subject to spurious branch attraction than are nonadditive multistate characters; Albert et al., 1993). As with mapped restriction site data, the probabilities of gain versus loss of a recognition string are highly asymmetrical, with parallel gains the least likely transformation series (Templeton, 1983; DeBry & Slade, 1985; Albert et al., 1992a). Therefore, string data may contain historical markers much less likely to engage in branch attraction (which occurs because of accumulated parallelisms; cf. Felsenstein, 1978; Hendy & Penny, 1989;

[10] Patterns of codon usage intrinsic to the primary nucleotide matrix are also suggestive of functional constraints; these are discussed in a separate paper (Albert, Backlund & Bremer, in press).

TABLE 3. Analysis of character support for internal branches of tree #1 (of 8) from the nucleotide analysis. "Node" refers to the node numbers on the reference tree of Appendix I. "# changes" refers to the total number of nucleotide changes optimized onto a branch. "Constant" indicates that the nucleotide site belongs in a codon position that codes for the same amino acid throughout the entire matrix. "No change" indicates that the nucleotide site belongs in a codon position that codes for two or more amino acids throughout the matrix, but that the particular change indicated at this node does not cause a change in amino acid sequence. "Labile" means that the inferred change in amino acid due to the observed change in nucleotide sequence is likely to happen by random chance or better (according to the PAM-250 log-odds matrix of Dayhoff et al., 1978: 352). "Potentially nonlabile" indicates that at least one of the potential amino acid changes inferred from a particular nucleotide position is not likely to happen by random, but that there also are some changes in the same character that are likely to happen by random chance or better. "Nonlabile" means that all inferred acid changes (often only one) occur at less than random chance.

Node	# changes	Constant	No change	Labile	Potentially nonlabile	Nonlabile
78–77	42	22	4	8	5	3
77–76	24	13	6	4	0	1
76–71	27	13	9	3	2	0
71–70	29	19	9	1	0	0
70–42	40	24	11	5	0	0
42–41	33	26	5	1	0	1
70–69	42	17	16	8	0	1
69–66	29	21	8	0	0	0
66–48	34	15	13	5	0	1
48–44	25	10	12	2	0	1
44–43	29	19	8	2	0	0
48–47	15	7	8	0	0	0
47–46	24	14	7	3	0	0
46–45	11	4	4	3	0	0
66–65	56	34	15	7	0	0
65–64	26	13	10	3	0	0
64–63	18	11	6	1	0	0
63–54	5	2	0	3	0	0
54–53	4	3	0	1	0	0
53–51	10	3	1	5	1	0
51–49	9	4	2	3	0	0
51–50	8	2	1	5	0	0
53–52	11	5	2	4	0	0
63–62	16	11	5	0	0	0
62–61	14	6	7	1	0	0
61–59	8	2	4	2	0	0
59–58	17	8	5	4	0	0
58–57	13	6	4	3	0	0
57–56	33	20	6	7	0	0
56–55	6	3	2	1	0	0
61–60	8	5	2	1	0	0
69–68	58	29	18	8	3	0
68–67	45	24	17	4	0	0
76–75	34	20	7	4	0	3
75–74	38	23	12	2	1	0
74–73	45	28	14	3	0	0
73–72	65	43	12	9	1	0
Σ	951	529	272	126	13	11
	100.00%	55.63%	28.60%	13.25%	1.37%	1.16%
		84.23%				
		97.48%				

Albert et al., 1992a, 1993) and much more likely to contain "blocks" of evolutionarily correlated information. Nevertheless, this information could be functionally constrained, as with primary nucleotide data. This possibility can be studied similarly by examining inferred amino acid changes on cladograms; each string character is easily traced to its recognized codons and component nucleotides.

Data analysis. One thousand random strings were generated for evaluation (see Appendix II). After scanning the 40 *rbc*L sequences, 193 positionally distinct string recognitions were recorded (mostly from small strings, the largest being from a 15-mer; see Appendix II). Of these, 112 identified two or more taxa. As there was no control in our procedure for string overlap, a number of string recognitions are non-independent with respect to nucleotides identified (see Appendix II). Therefore, our string data carry an experimental bias similar to what could occur with restriction site data representing mapped cleavage points for several endonucleases. The "supersites" string transform (J. S. Farris, unpublished) avoids this difficulty entirely, and if modified for the production of presence/absence data, would be identical to our intent but superior in execution. Nevertheless, our string data should suffice to explore biological non-independence of nucleotides (functional constraints); in fact, partial replication of nucleotide "blocks" could enhance detection of conserved regions. Cladistic analysis of the string characters was performed under the Wagner criterion (Kluge & Farris, 1969; Farris, 1970; see Albert et al., 1992a) using the same program and options mentioned previously; 165 equally parsimonious trees were found ($C = 0.381$ (including all data), $R = 0.524$). The combinable component consensus tree differs from the strict by only one component (see Fig. 4).

The string data provide a different resolution of land-plant relationships than the nucleotide sequences (Figs. 3, 4). Notable differences include (i) *Equisetum* placed among the bryophytes, (ii) paraphyly of *Psilotum* + ferns and paraphyly of lycopods, (iii) sister-group status of Gnetales to angiosperms (with *Piper* basalmost), and (iv) paraphyly of angiosperms to conifers + (*Ginkgo*, cycads). Characteristics (i) and (iv) are in total conflict with other results (listed under Nucleotides, above), whereas (ii–iii) are not.

Function and phylogeny. It could be argued that cladograms produced from string-transformed data are better phylogenetic representations than those derived from nucleotides because the unit character is substantially less subject to parallel gains (see above). However, this attribute is distinct from the nature of the history conserved by string data; whole functional units may be incorporated into single characters. Gross differences in tree topology (including paraphyly of angiosperms) may simply result from different representations of functional and phylogenetic history in string versus nucleotide data forms.

We have studied possible functional constraints on *rbc*L evolution (as above) by examining the inferred amino acid changes on the internal branches of one of the 165 equally most-parsimonious string trees (Appendix II). Striking differences from the nucleotide-based analysis (Table 3) are shown in Table 4: only 45% of string transformations (changes in underlying nucleotide sequence) are silent with regard to amino acid identity (versus ca. 84% in the nucleotide analysis, a decrease by half), and functionally labile amino acid replacements amount to an additional 25% (versus ca. 13% in the nucleotide analysis, a relative increase). Thus, 70% of underlying nucleotide changes appear to be functionally neutral, whereas non-labile amino acid replacements amount to a maximum of 28% (an additional 2.1% are ascribed to internal stop codons, which may result from sequencing errors). This greater number of presumably functional changes in underlying nucleotides does indicate a greater chance that functional associations among particular nucleotides may bias tree construction.

The different substitutional patterns between nucleotide and string data can be explained by inherent properties of the latter. Each string recognition shared by two or more sequences comprises much more inclusive and conservative information than shared nucleotide identity at a given site. From our previous arguments about functional constraints in *rbc*L sequence evolution (see The Rate "Problem" and Nucleotides, above), the majority of string recognitions are expected to identify functionally conserved nucleotide motifs. The proportional reduction in discernible silent substitutions on the nucleotide level is likely due to the increased size of the functional units compared; with a 6 base-pair string, the chance of observing a non-silent change is at least six times greater than for a single nucleotide position. The proportional increase in labile amino acid replacements can be explained through similar reasoning; if a string recognition identifies a functionally conserved motif, the larger the motif, the greater the likelihood that functional preservation need not require exact

TABLE 4. Analysis of character support for internal branches of tree #100 (of 165) from the string analysis. "Node" refers to the node numbers on the reference tree of Appendix II. "# changes" refers to the total number of string changes optimized onto a branch. "Constant" indicates that the string identifies codon positions that code for the same amino acid throughout the entire matrix. "Labile" means that the inferred change in amino acid due to the observed change in string recognition is likely to happen by random chance or better (according to the PAM-250 log-odds matrix of Dayhoff et al., 1978: 352). "Potentially nonlabile" indicates that at least one of the potential amino acid changes inferred from a particular string recognition is not likely to happen by random, but that there also are some changes in the same character that are likely to happen by random chance or better. "Nonlabile" means that all inferred amino acid changes (often only one) occur at less than random chance. "Internal stop" refers to string recognitions that identify internal stop codons, which may be sequencing artifacts.

Node	# changes	Constant	Labile	Potentially nonlabile	Nonlabile	Internal stop
77–76	7	3	3	1	0	0
76–75	7	5	2	0	0	0
75–74	6	1	1	2	1	1
74–73	4	4	0	0	0	0
73–72	4	4	0	0	0	0
72–42	4	2	2	0	0	0
42–41	9	4	3	1	1	0
72–71	4	1	1	2	0	0
71–70	6	4	2	0	0	0
70–43	5	1	1	3	0	0
70–69	2	2	0	0	0	0
69 66	7	3	1	3	0	0
66–65	4	1	1	0	2	0
65–51	3	1	1	0	0	1
51–50	3	1	1	1	0	0
50–49	6	4	2	0	0	0
49–48	8	3	3	0	1	1
48–44	6	3	1	0	2	0
48–47	4	1	0	2	1	0
47–46	8	2	3	1	2	0
46–45	3	2	0	0	1	0
65–64	4	1	2	0	1	0
64–55	3	1	1	0	1	0
55–54	2	0	1	0	1	0
54–52	1	1	0	0	0	0
54–53	3	2	0	0	1	0
64–63	1	1	0	0	0	0
63–62	4	1	1	1	1	0
62–61	2	0	0	0	2	0
61–56	2	0	1	1	0	0
60 57	2	1	0	0	1	0
60–59	5	1	2	1	1	0
59–58	2	1	1	0	0	0
69–68	4	1	1	1	0	1
68–67	10	6	1	1	2	0
Σ	155	69	39	21	22	4
	100.00%	44.51%	25.16%	13.55%	14.19%	2.08%
		69.67%		27.74%		

amino acid identity. Strings recognizing regions of non-labile change, indicating potentially radical changes in structure and function among taxa, may represent another class of conserved information. Again, these are probably found in greater proportion because of the larger size of the unit characters. Rather than being conserved because of functional constraints (as above), such recognitions

may identify conserved markers for historical groups. Such changes may or may not have drastic physiological effects (see Hudson et al., 1990, on *rbc*L ; cf. Perutz & Lehman, 1968; Nei, 1987: 270–271), but they could be of similar phylogenetic utility as chloroplast DNA rearrangements (e.g., Jansen & Palmer, 1987; Palmer et al., 1988; Bruneau et al., 1990; Lavin et al., 1990; Downie & Palmer, 1992; Downie et al., 1991; Raubeson & Jansen, 1992) if well characterized in relation to the crystal structure of the large-subunit protein (Chapman et al., 1988; Andersson et al., 1989; cf. Clegg, 1993).

AMINO ACIDS

Because *rbc*L nucleotide substitutions approximate a clock hypothesis (see The Rate "Problem," above), amino acid changes are expected to conform to the neutral hypothesis of molecular evolution (see Nei, 1987: 47–59, 409–412), although we do not directly address this issue here. Direct inference of trees can proceed from amino acids (yet another transformation of the same primary evidence). One limitation of using the amino acid sequences themselves is the "factoring-out" of all synonymous variation at the nucleotide level; this again may make it more likely that functional associations among characters may bias tree construction. Topological resolution may also be limited because amino acid data is optimized nonadditively (Fitch, 1971) and more than four states could be available for given characters (in the *rbc*L sequences examined here, the maximum is six states at four different positions). Nevertheless, the greater the number of character states, the lower the probability of character-state parallelism and spurious branch attraction (Albert et al., 1993). It could thus be argued that amino acid data might be more suitable for bridging large evolutionary time gaps, given a roughly constant rate of substitution combined with ignorance of potentially multiple synonymous nucleotide changes. Hence, we evaluated the amino acid data for hierarchic compatibility with the results of the nucleotide and string analyses.

Data analysis. After "translating" the 40 *rbc*L sequences, 66 (out of the 476) amino acid positions identified two or more taxa. Cladistic analysis of these characters was performed under the Fitch criterion (Fitch, 1971) using the same program and options mentioned previously; 104 equally parsimonious trees were found ($C = 0.567$ (including all data), $R = 0.554$). The combinable component consensus tree preserved one more component than the strict (see Fig. 5).

The amino acid data provide yet another resolution of land-plant relationships (cf. Figs. 3, 4): (i) lycopods are polyphyletic, with *Isoetes* sister to *Angiopteris*, (ii) *Anthoceros* is embedded among fern allies, (iii) gymnosperms as a whole (with conifers polyphyletic) are the monophyletic sister group to angiosperms (with *Nymphaea* basalmost), and (iv) *Lilium* is sister to *Dillenia*. Except for gymnosperm monophyly as hypothesized from rDNA data (see Troitsky et al., 1991) these characteristics are in total conflict with all previous studies (listed under Nucleotides, above).

From the arbiter of congruence, large-subunit amino acid data are no more appropriate for bridging gaps in asymmetric time samples than nucleotide or string data. As argued above, the clocklike behavior of *rbc*L nucleotide substitution is expected to obtain also in the translated amino acid data; thus, λ values for amino acid changes (and so the likelihood of spurious branch attraction) should also be sensitive to differences in divergence times.

Function and phylogeny. Amino acid changes in *rbc*L are apparently subject to strong functional constraints (see Nucleotides and Strings, above). One could argue that amino acid data is less subject to the "noise" of neutrality, i.e., multiple silent changes at given nucleotide positions. However, selective neutrality may be roughly maintained by labile amino acid replacements, which could similarly "wobble" back and forth across evolutionary time. Only a small percentage of individual amino acids appears to be involved in function-changing evolutionary events (see Nucleotides, above).

PENULTIMATE CONCLUSIONS

We have demonstrated the problematic, functionally constrained nature of *rbc*L markers currently being used for phylogeny estimation by many workers. Three transformations of the same evidence produced discordant cladistic topologies and substantial incongruence with previous morphological cladistic results. Of course, we do not suggest that the growing *rbc*L database be abandoned. Rather, we suggest (as will be elaborated below) that all investigators involved with *rbc*L or other gene data take heed of standard and powerful cladistic procedures for discriminating cladistic history (homology) from homoplasy (functional parallelism and reversal).

Total Evidence and Character Congruence

(I) on characters

Every character in a data matrix showing similarity between two or more taxa is optimized under parsimony as a discrete and independent piece of information. This holds whether or not the character represents a single taxic homology or only a portion of one (which is the case with correlated or contingent characters). A taxic homology used in parsimony analysis is expected to have a single functional history (even if this history changes over time; see Riedl, 1978; Donoghue, 1989; Donoghue & Sanderson, 1992); its cladistic utility (i.e., optimization as synapomorphy or homoplasy) is tested at maximum parsimony along with all other characters in a matrix. From our argument about shared functional history (constraints) in the evolution of *rbc*L, one might be tempted to equate a given taxic homology (e.g., nuclear versus cellular endosperm development) with the entire *rbc*L gene. However, unlike a given taxic homology, *rbc*L is composed of multiple, discrete points of information, that is, its ca. 1428 nucleotides. To a parsimony algorithm, each of these data points is equivalent to the single, nonadditive taxic homology statement "functional pollen unit in the Orchidaceae: monad, tetrad, massula, or pollinium," whatever its underlying complexity.

Hence, some workers have found cladistic philosophy and methodology at an impasse. For example, it has been argued that gene information could be combined with other characters either through multistate recoding of gene trees (Doyle, 1992) or through analysis of component compatibility among separately produced cladograms (Page, 1993). Legitimate concern over potentially separate phylogenetic histories led to these suggestions, but we argue below that both approaches unnecessarily restrict the information content of cladistic hierarchies, a feature fundamental to the superiority of parsimony methods (see Farris, 1979, 1983); in fact, parsimony itself arbitrates the supposed analytical quandary.

(II) on evidence

For cladistic analysis, evidence is the body of available information that shows patterns of similarity among terminals. A specific set of evidence may be expressed in different forms; we have shown this property through different data transformations of the *rbc*L gene (above). Approaches that combine evidence in the form of tree components do so at the cost of information content (for recent debate on this issue, see Jones et al., 1993; Nelson, 1993; Barrett et al., 1993; De Queiroz, 1993). In fact, acceptance of parsimony as the arbiter of synapomorphy and homoplasy seems methodologically counterintuitive to component combination, which does not directly use such information (see Doyle, 1992; Page, 1993). Parsimony, acting over all evidence, will provide estimates of congruence among character-state patterns while minimizing ad hoc assumptions (Farris, 1983). For example, some characters from a multigene family (gene duplication being part of the functional burden) may not show congruence with the body of retained synapomorphy because of paralogous histories (Fitch, 1970). Nevertheless, analysis of "total" evidence (sensu Kluge, 1989) gives each data point the opportunity both to affect hierarchy directly and to be diagnosed objectively, which is not the case when evidence is decomposed a priori and later combined or reconciled (cf. Doyle, 1992; Page, 1993). In conclusion, although a functionally constrained DNA sequence like the *rbc*L gene may appear to deserve the same rank as a given morphological character, it is more evidence-rich, and all of this evidence can be examined for hierarchic correlation (sensu Farris, 1969) with other data.

(III) an example

The extent to which *rbc*L evidence shows hierarchic correlation with other evidence should provide an objective measure of its freedom from biasing functional considerations, and consequentially, its phylogenetic utility. In this context, we examined character interaction between *rbc*L evidence and the primarily morphological seed-plant matrix of Nixon et al. (1994). Using the set of functional histories in the morphological matrix as a "constant," we tested the ability of different *rbc*L data forms (i.e., nucleotides, strings, and amino acids) to produce a unified representation of the same evidence. Two different sets of experiments were performed: (i) analyses including fossil taxa for which *rbc*L evidence is lacking (and therefore coded as missing data), and (ii) analyses of data for extant taxa only (the intersection of available evidence). To measure character congruence, we have used the retention index: the proportion of congruent similarity (i.e., synapomorphy) in a data matrix that is retained at maximum parsimony (see Farris, 1989a, b, 1991). Although retention is not directly comparable among different data matrices (see Goloboff, 1991), each matrix within our respective sets of experiments shares the same "constant." Additionally, each data transform of *rbc*L

TABLE 5. Homoplasy and character congruence statistics for total evidence analyses comprising morphological (Nixon et al., 1994; matrix version as of 8 November 1993) and *rbc*L data. Consistency (over all data) and retention indices are listed (see text), along with the number of trees found (see Figs. 6–8). For comparisons involving both fossil and extant taxa, 101 morphological similarities are relevant (symbolized by "N"); for extants only, there are 96 (symbolized by "N_{ex}"). The numbers of relevant similarities for each *rbc*L data transform (nucleotides, strings, amino acids) are given in the text. For analyses including fossil taxa, *rbc*L evidence was represented as missing (i.e., "?").

	Consistency	Retention	# Trees
Fossil plus extant taxa			
N + nucleotides	0.450	0.625	44
N + strings	0.402	0.685	22
N + amino acids	0.467	0.710	309
Extant taxa only			
N_{ex} + nucleotides	0.464	0.601	3
N_{ex} + strings	0.442	0.641	7
N_{ex} + amino acids	0.518	0.670	24

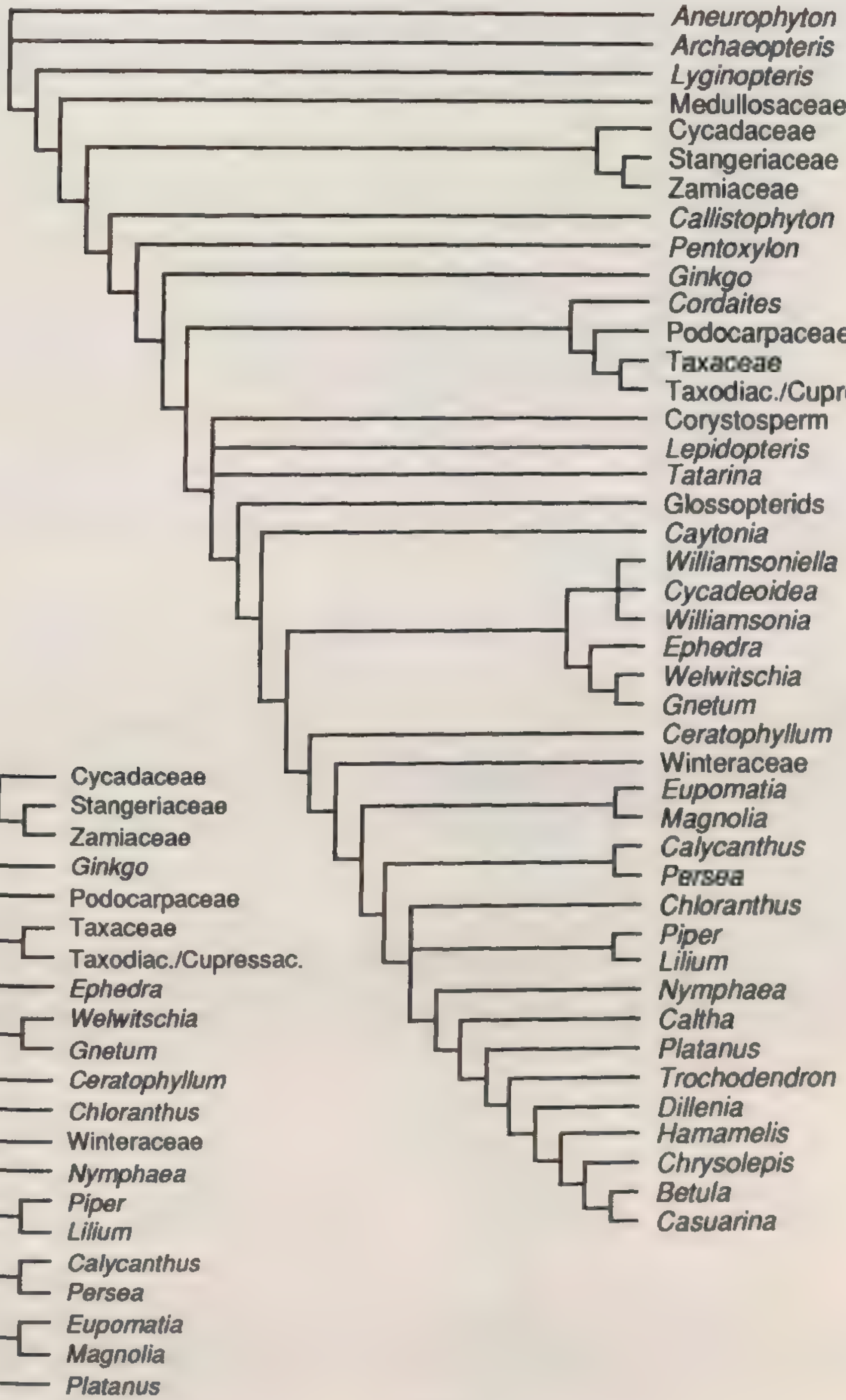
is assumed to be evidentially equivalent until shown otherwise (this assumption is obviously weaker for the string data, as they do not represent a completely saturated transformation of the nucleotide sequences). Finally, we do not use retention to suggest which analysis(es) may be "better."

The characters and cladistic reconstructions for living and fossil seed plants are described elsewhere (Nixon et al., 1994). We used the same parsimony methods outlined above to examine six combined matrices comparing all versus extant-only taxa and nucleotide/string/amino-acid *rbc*L data in all combinations. Consistency and retention indices for each analysis are reported in Table 5, and topological results are summarized in Figures 6–8. Character congruence, as measured through retention, is similar in magnitude (range < 0.1) across each set of experiments. Although topological resolution and component placements differ somewhat with respect to the *rbc*L data form used (Figs. 6–8; see Nixon et al., 1994), the *rbc*L evidence appears to be making a consistent statement along with the morphological evidence.

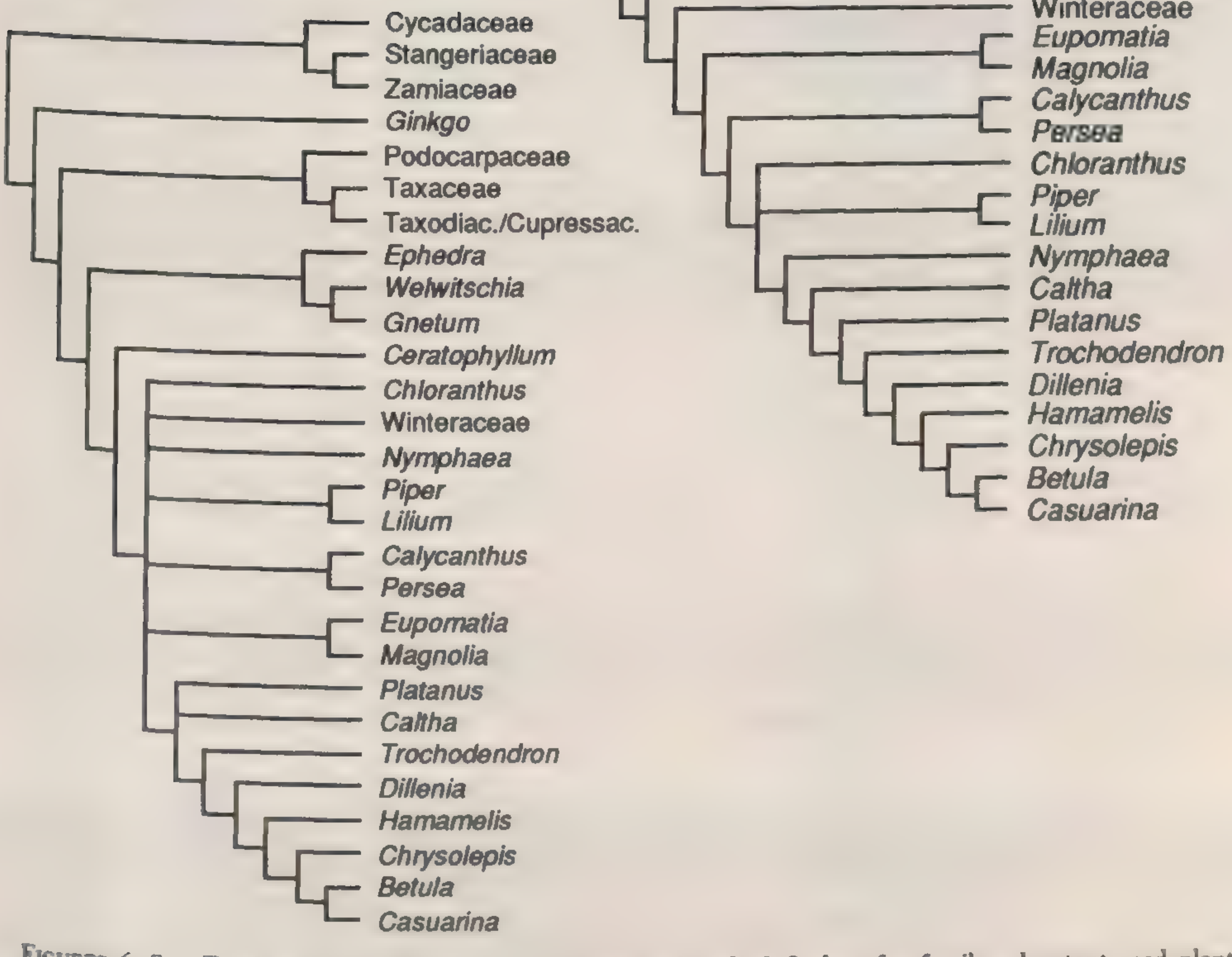
With respect to extant taxa, monophyletic cycads are the most topologically ancestral in all analyses including fossils (Figs. 6a–8a). *Ginkgo* appears either external to *Cordaites* plus conifers (Figs. 6a, 7a) or monophyletic with these taxa (Fig. 8a). In extant-only analyses, *Ginkgo* similarly intercalates between cycads and conifers (Figs. 6b, 7b) or remains sister to conifers (Fig. 8b). Conifers themselves are monophyletic in most combined analyses (Figs. 6a, b, 7a, 8a, b), but are partially unresolved in the extant-only analysis with string data (Fig. 7b). Every analysis resolves the Gnetales and Bennettitales as sister to the angiosperms. *Ephedra* is uniformly sister to *Gnetum* plus *Welwitschia*, but resolution within Bennettitales is provided only in the combined analysis with amino acid data (Fig. 8a). *Ceratophyllum* is placed sister to all other angiosperms (see Les, 1988; Chase et al., 1993; Qiu et al., 1993) in the combined nucleotide and string analyses (Figs. 6a, b, 7a, b), but not in the combined amino acid analyses (Fig. 8a, b), where it either nests well within angiosperms (sister to *Chloranthus*; Fig. 8a) or remains unresolved (Fig. 8b). Indeed, relationships within the angiosperms are the least stable among the combined data analyses. Woody magnoliids occupy the basalmost branches in Figure 6a, whereas the "paleoherb" taxon *Nymphaea* occupies this position in Figure 7a, and all other analyses are indecisive on this point. Eudicots (angiosperms with triaperturate or triaperturate-derived pollen; here, *Platanus*, *Caltha*, *Trochodendron*, *Dillenia*, *Hamamelis*, *Chrysolepis*, *Betula*, *Casuarina*) are monophyletic in the combined nucleotide and string analyses (Figs. 6a, b, 7a, b) (see Chase et al., 1993) but are polyphyletic in the combined amino acid analyses (Fig. 8a, b). For further discussion and reference to cladograms based solely on the morphological evidence, see Nixon et al. (1994).

The topological differences resulting from use of either *rbc*L nucleotide, string, or amino acid data might imply that different sets of morphological characters (of Nixon et al., 1994) show congruence with these different data forms. If one were to hold the evidential significance of the morphological data constant, one might identify those portions of primary *rbc*L nucleotide sequence that were incongruent under each data form and ignore them in future studies. Alternatively, one could take the opposite approach and ignore those Nixon et al. (1994) characters that were not congruent among all *rbc*L data forms. We suggest that either approach is nihilistic with respect to either *rbc*L or morphology; because congruence is an aspect of total interaction, the utility of either set of evidence is always judged relative to the other. Nevertheless, hierarchic correlation can be directed at one subset of total evidence if, as in the case of *rbc*L, it is reasonable to assume a single, unifying functional history. If an investigator were willing to hold all evidence except *rbc*L constant, hypotheses of correlation between functional constraints

6(a)

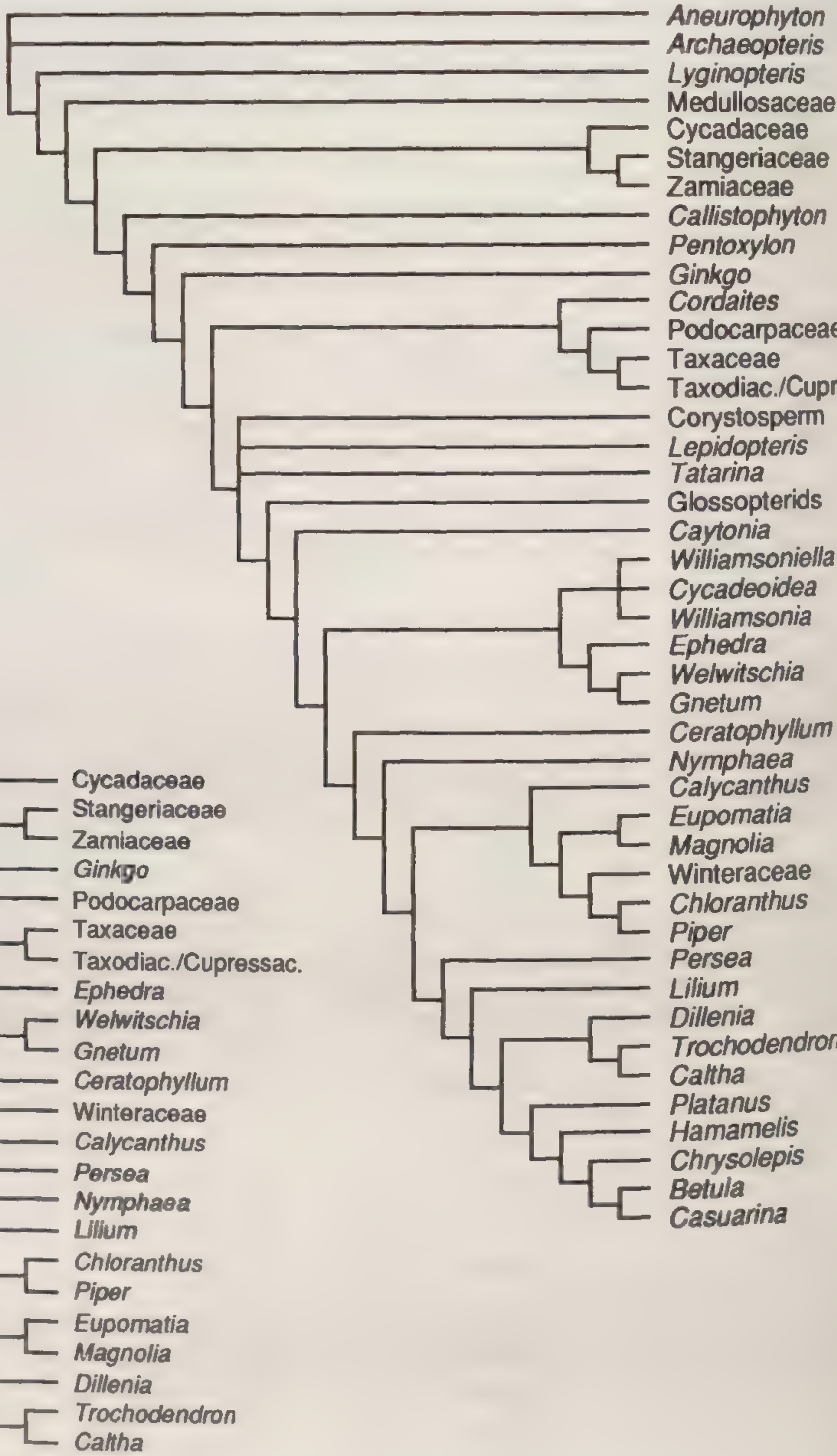


6(b)

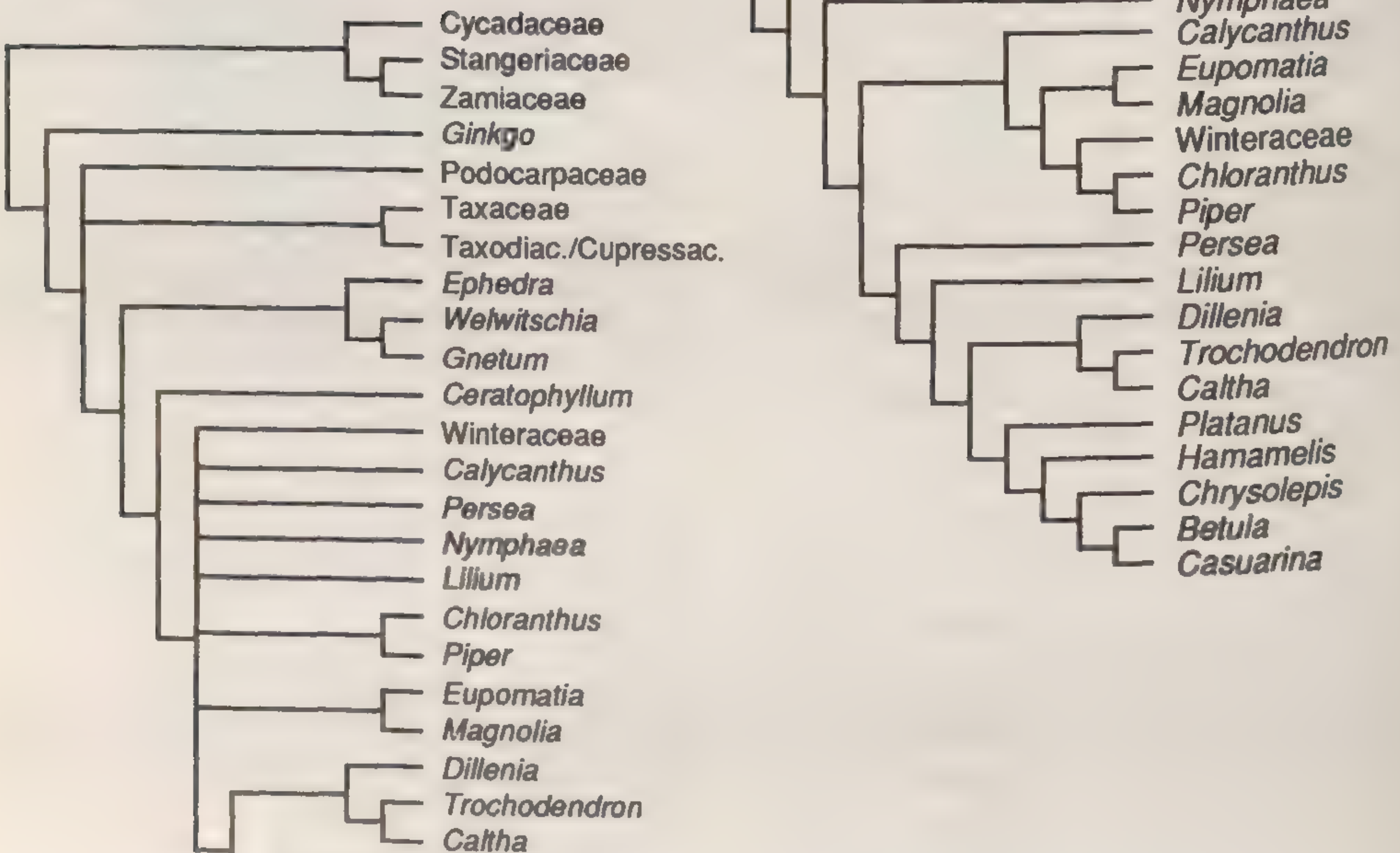


FIGURES 6–8. Total evidence analyses of morphological and *rbc*L data for fossil and extant seed plants. The morphological data and taxon sampling of Nixon et al. (1994; matrix version as of 8 November 1993) was followed for cladistic analyses of fossil and living seed plants (the "a" series) and of extant seed plants only (the "b" series). For both taxonomic scopes, *rbc*L evidence was combined as one of three data forms: nucleotide sequences (6), nucleotide string recognitions (7), or amino acid sequences (8) obtained from single organisms (see Table 2). For →

7(a)

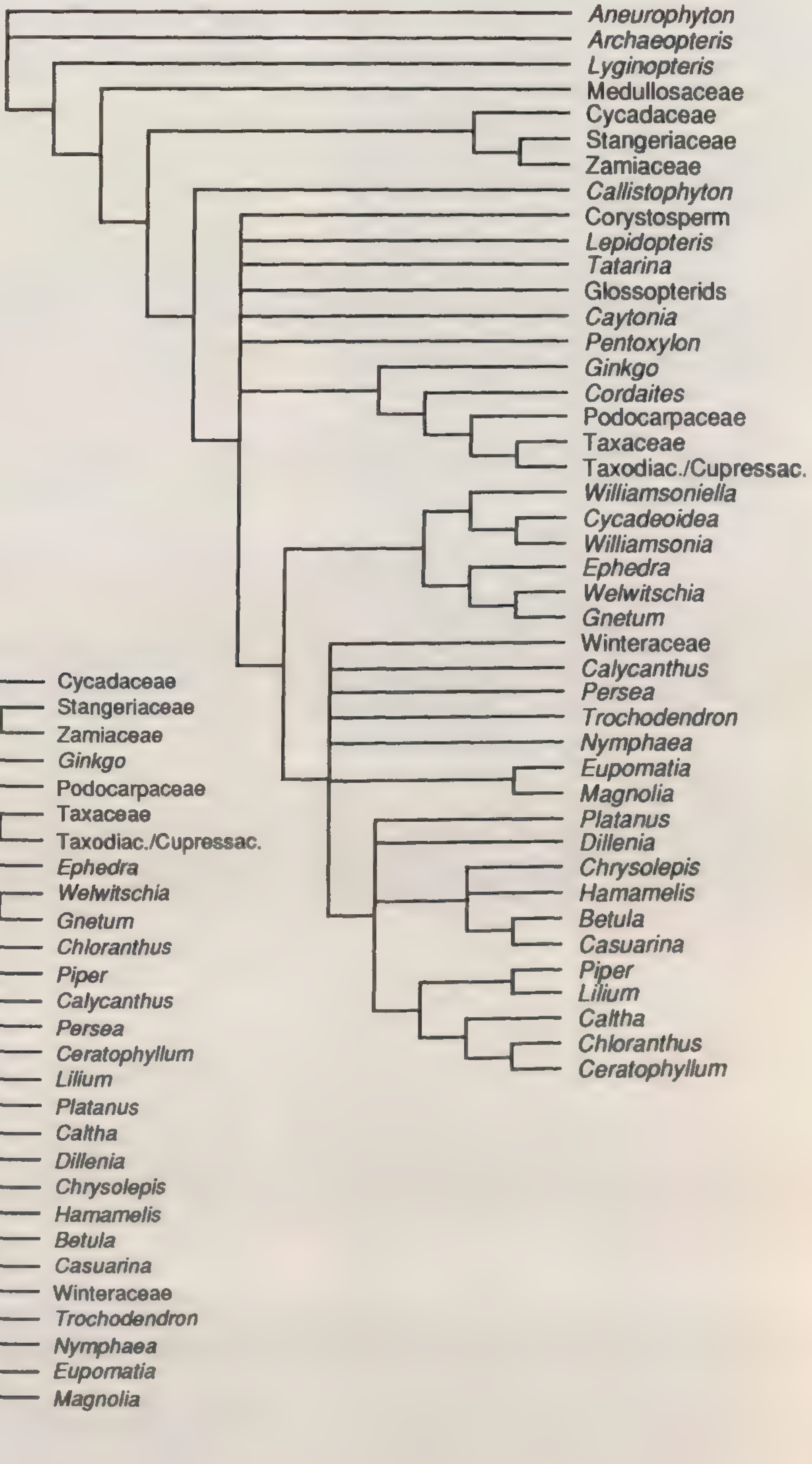


7(b)

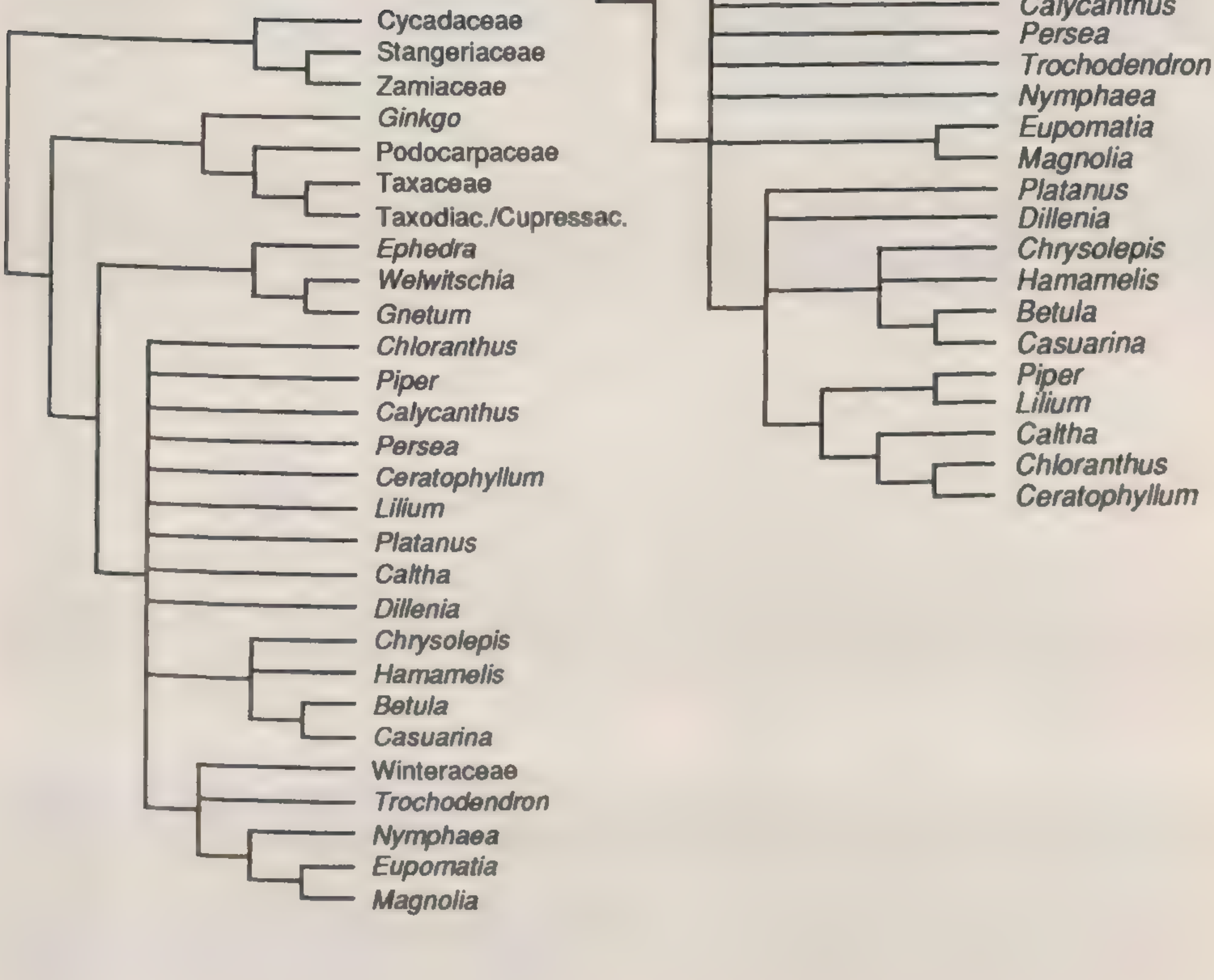


analyses including fossil taxa, *rbc*L character states were scored as missing (i.e., "?"; cf. Platnick et al., 1991; Swofford, 1993: 21–24). Topological results (from PAUP 3.1.1; Swofford, 1993) shown represent either single trees or the strict consensus (= combinable component consensus in all cases) of all most-parsimonious trees found (see Table 5). See text for further discussion.

8(a)


Aneurophyton
Archaeopteris
Lyginopteris
Medullosaceae
Cycadaceae
Stangeriaceae
Zamiaceae
Callistophyton
Corystosperm
Lepidopteris
Tatarina
Glossopterids
Caytonia
Pentoxylon
Ginkgo
Cordaites
Podocarpaceae
Taxaceae
Taxodiac./Cupressac.
Williamsoniella
Cycadeoidea
Williamsonia
Ephedra
Welwitschia
Gnetum
Winteraceae
Calycanthus
Persea
Trochodendron
Nymphaea
Eupomatia
Magnolia
Platanus
Dillenia
Chrysolepis
Hamamelis
Betula
Casuarina
Piper
Lilium
Caltha
Chloranthus
Ceratophyllum

8(b)


Cycadaceae
Stangeriaceae
Zamiaceae
Ginkgo
Podocarpaceae
Taxaceae
Taxodiac./Cupressac.
Ephedra
Welwitschia
Gnetum
Chloranthus
Piper
Calycanthus
Persea
Ceratophyllum
Lilium
Platanus
Caltha
Dillenia
Chrysolepis
Hamamelis
Betula
Casuarina
Winteraceae
Trochodendron
Nymphaea
Eupomatia
Magnolia

and phylogenetic history could be generated from the congruence patterns of each *rbc*L character.

Conclusions

The phylogenetic informativeness of *rbc*L variation is obviously subject to any special properties the gene may have. Unlike for most morphological characters, some such properties can be listed for *rbc*L with confidence: (i) *rbc*L nucleotides show clocklike substitutional behavior, which may either help or hinder tree reconstruction depending upon the temporal depth and asymmetry of a given phylogenetic question; (ii) strong functional constraints exist over the majority of informative nucleotide characters, which is expected from (i) under the neutral theory; and (iii) the form that *rbc*L evidence takes (e.g., nucleotides, strings, or amino acids) does not appreciably affect its interaction with other evidence containing diverse functional histories (e.g., morphological data).

Although *rbc*L trees often appear consistent with taxonomic opinion (or are substantially congruent with other cladistic topologies), their power as lone cladistic tools will always be restricted by the intrinsic limits of internal evaluation of data. Because *rbc*L sequences clearly have a unifying functional history, simultaneous study of *all* available evidence become imperative. Functional constraints on *rbc*L, rDNA, or endosperm evolution are not expected to be similar; therefore patterns of character congruence among such diverse information sources will provide hypotheses of cladogenetic history significantly more powerful than studies of *rbc*L alone.

Literature Cited

Albert, V. A. & B. D. Mishler. 1992. On the rationale and utility of weighting nucleotide sequence data. Cladistics 8: 73–83.

———, A. Backlund & K. Bremer. DNA characters and cladistics: The optimization of functional history. *In* Models in Phylogenetic Reconstruction. The Systematics Association, Oxford Univ. Press. (in press).

———, M. W. Chase & B. D. Mishler. 1993. Character-state weighting for cladistic analysis of protein-coding DNA sequences. Ann. Missouri Bot. Gard. 80: 752–766.

———, B. D. Mishler & M. W. Chase. 1992a. Character-state weighting for restriction site data in phylogenetic reconstruction, with an example from chloroplast DNA. Pp. 369 403 *in* P. S. Soltis, D. E. Soltis & J. J. Doyle (editors), Molecular Systematics of Plants. Chapman and Hall, New York.

———, K. Bremer, M. W. Chase, J. Manhart, B. D. Mishler & K. C. Nixon. 1992b. *rbc*L gene sequences and phylogenetic studies of vascular plants. Pp. 13–14 *in* program booklet, "Origin and Relationships of the Major Plant Groups," 39th Annual Systematics Symposium, Missouri Bot. Gard., St. Louis [abstract].

———, S. E. Williams & M. W. Chase. 1992c. Carnivorous plants: Phylogeny and structural evolution. Science 257: 1491–1495.

Andersson, I., S. Knight, G. Schneider, Y. Lindqvist, T. Lundqvist, C.-I. Bränden & G. H. Lorimer. 1989. Crystal structure of the active site of ribulose-bisphosphate carboxylase. Nature 337: 229–234.

Barrett, M., M. J. Donoghue & E. Sober. 1991. Against consensus. Syst. Zool. 40: 486–493.

———, ——— & ———. 1993. Crusade? A reply to Nelson. Syst. Biol. 42: 216–217.

Bousquet, J., S. H. Strauss, A. D. Doerksen & R. A. Price. 1992. Extensive variation in evolutionary rate of *rbc*L gene sequences among seed plants. Proc. Natl. Acad. Sci. U.S.A. 89: 7844–7848.

Bremer, B. & K. Bremer. 1989. Cladistic analysis of blue-green procaryote interrelationships and chloroplast origin based on 16S rRNA oligonucleotide catalogues. J. Evol. Biol. 2: 13–30.

Bremer, K. 1985. Summary of green plant phylogeny and classification. Cladistics 1: 369–385.

———. 1990. Combinable component consensus. Cladistics 6: 369–372.

Bruneau, A., J. J. Doyle & J. D. Palmer. 1990. A chloroplast DNA inversion as a subtribal character in the Phaseolae (Leguminosae). Syst. Bot. 15: 378-386.

Chapman, M. S., S. W. Suh, P. M. G. Curmi, D. Cascio, W. W. Smith & D. S. Eisenberg. 1988. Tertiary structure of plant RuBisCo: Domains and their contacts. Science 241: 71–74.

Chase, M. W., D. E. Soltis, R. G. Olmstead, D. Morgan, D. H. Les, B. D. Mishler, M. R. Duvall, R. A. Price, H. G. Hills, Y.-L. Qiu, K. A. Kron, J. H. Rettig, E. Conti, J. D. Palmer, J. R. Manhart, K. J. Sytsma, H. J. Michaels, W. J. Kress, K. G. Karol, W. D. Clark, M. Hedrén, B. S. Gaut, R. K. Jansen, K.-J. Kim, C. F. Wimpee, J. F. Smith, G. R. Furnier, S. H. Strauss, Q.-Y. Xiang, G. M. Plunkett, P. S. Soltis, S. Swensen, S. E. Williams, P. A. Gadek, C. J. Quinn, L. E. Eguiarte, E. Golenberg, G. H. Learn, Jr., S. W. Graham, S. C. H. Barrett, S. Dayanandan & V. A. Albert. 1993. Phylogenetics of seed plants: An analysis of nucleotide sequences from the plastid gene *rbc*L. Ann. Missouri Bot. Gard. 80: 528–580.

Clegg, M. T. 1993. Chloroplast gene sequences and the study of plant evolution. Proc. Natl. Acad. Sci. U.S.A. 90: 363–367.

——— & G. Zurawski. 1992. Chloroplast DNA and the study of plant phylogeny: Present status and future prospects. Pp. 1–13 *in* P. S. Soltis, D. E. Soltis & J. J. Doyle (editors), Molecular Systematics of Plants. Chapman and Hall, New York.

Conti, E., A Fischbach & K. J. Sytsma. 1993. Tribal relationships in Onagraceae: Implications from *rbc*L sequence data. Ann. Missouri Bot. Gard. 80: 672-685.

Crane, P. R. 1985. Phylogenetic analysis of seed plants and the origin of angiosperms. Ann. Missouri Bot. Gard. 72: 716 793.

Dayhoff, M. O., R. M. Schwartz & B. C. Orcutt. 1978. A model of evolutionary change in proteins. Pp. 345–352 *in* M. O. Dayhoff (editor), Atlas of

Protein Sequence and Structure, Vol. 5, Suppl. 3. National Biomedical Research Foundation, Washington, D.C.

DeBry, R. W. & N. A. Slade. 1985. Cladistic analysis of restriction endonuclease cleavage maps within a maximum-likelihood framework. Syst. Zool. 34: 24–34.

De Queiroz, A. 1993. For consensus (sometimes). Syst. Biol. 42: 368–372.

Donoghue, M. J. 1989. Phylogenies and the analysis of evolutionary sequences, with examples from seed plants. Evolution 43: 1137–1156.

——— & J. A. Doyle. 1989. Phylogenetic analysis of angiosperms and the relationships of Hamamelidae. Pp. 17–45 *in* P. R. Crane & S. Blackmore (editors), Evolution, Systematics, and Fossil History of the Hamamelidae, Volume 1: Introduction and "Lower" Hamamelidae. Clarendon Press, Oxford.

——— & M. J. Sanderson. 1992. The suitability of molecular and morphological evidence in reconstructing plant phylogeny. Pp. 340 368 *in* P. S. Soltis, D. E. Soltis & J. J. Doyle (editors), Molecular Systematics of Plants. Chapman and Hall, New York.

Downie, S. R. & J. D. Palmer. 1992. Use of chloroplast DNA rearrangements in reconstructing plant phylogeny. Pp. 14–35 *in* P. S. Soltis, D. E. Soltis & J. J. Doyle (editors), Molecular Systematics of Plants. Chapman and Hall, New York.

———, R. G. Olmstead, G. Zurawski, D. E. Soltis, P. S. Soltis, J. C. Watson & J. D. Palmer. 1991. Six independent losses of the chloroplast DNA *rpl*2 intron in dicotyledons: Molecular and phylogenetic implications. Evolution 45: 1245–1259.

Doyle, J. A. & M. J. Donoghue. 1986. Seed plant phylogeny and the origin of angiosperms: An experimental cladistic approach. Bot. Rev. 52: 321 431.

——— & ———. 1992. Fossils and seed plant phylogeny reanalyzed. Brittonia 44: 89–106.

Doyle, J. J. 1992. Gene trees and species trees: Molecular systematics as one-character taxonomy. Syst. Bot. 17: 144–163.

Farris, J. S. 1969. A successive approximations approach to character weighting. Syst. Zool. 18: 374 385.

———. 1970. Methods for computing Wagner trees. Syst. Zool. 19: 83–92.

———. 1978. Inferring phylogenetic trees from chromosome inversion data. Syst. Zool. 27: 275–284.

———. 1979. The information content of the phylogenetic system. Syst. Zool. 28: 483–519.

———. 1983. The logical basis of phylogenetic analysis. Pp. 7–36 *in* N. I. Platnick & V. A. Funk (editors), Advances in Cladistics, Vol. 2. Columbia Univ. Press, New York.

———. 1989a. The retention index and the rescaled consistency index. Cladistics 5: 417–419.

———. 1989b. The retention index and homoplasy excess. Syst. Zool. 38: 406–407.

———. 1991. Excess homoplasy ratios. Cladistics 7: 81 91.

Felsenstein, J. 1978. Cases in which parsimony or compatibility methods will be positively misleading. Syst. Zool. 27: 401–410.

Fitch, W. M. 1970. Distinguishing homologous from analogous proteins. Syst. Zool. 19: 99–113.

———. 1971. Toward defining the course of evolution: Minimum change for specific tree topology. Syst. Zool. 20: 406–416.

———. 1986. The estimate of total nucleotide substitutions from pairwise differences is biased. Philos. Trans., Ser. B 316: 317–324.

——— & E. Markowitz. 1970. An improved method for determining codon variability in a gene and its application to the rate of fixation of mutations in evolution. Biochem. Genet. 4: 579–593.

Fox, G. E., E. Stackebrandt, R. B. Hespell, J. Gibson, J. Maniloff, T. A. Dyer, R. S. Wolfe, W. E. Balch, R. S. Tanner, L. J. Magrum, L. B. Zablen, R. Blakemore, R. Gupta, L. Bonen, B. J. Lewis, D. A. Stahl, K. R. Luehrsen, K. N. Chen & C. R. Woese. 1980. The phylogeny of prokaryotes. Science 209: 457–463.

Gaut, B. S., S. V. Muse, W. D. Clark & M. T. Clegg. 1992. Relative rates of nucleotide substitution at the *rbc*L locus of monocotyledonous plants. J. Molec. Evol. 35: 292–303.

Golenberg, E. M., D. E. Giannasi, M. T. Clegg, C. J. Smiley, M. Durbin, D. Henderson & G. Zurawski. 1990. Chloroplast DNA sequence from a Miocene *Magnolia* species. Nature 334: 656 658.

Goloboff, P. A. 1991. Homoplasy and the choice among cladograms. Cladistics 7: 215–232.

Hamby, R. K. & E. A. Zimmer. 1992. Ribosomal RNA as a phylogenetic tool in plant systematics. Pp. 50–91 *in* P. S. Soltis, D. E. Soltis & J. J. Doyle (editors), Molecular Systematics of Plants. Chapman and Hall, New York.

Hendy, M. D. & D. Penny. 1989. A framework for the quantitative study of evolutionary trees. Syst. Zool. 38: 297–309.

Hudson, G. S., J. D. Mahon, P. A. Anderson, M. J. Gibbs, M. R. Badger, T. J. Andrews & P. R. Whitfeld. 1990. Comparisons for *rbc*L genes for the large subunit of ribulose-bisphosphate carboxylase from closely related C_3 and C_4 plant species. J. Biol. Chem. 265: 808–814.

Jansen, R. K. & J. D. Palmer. 1987. Chloroplast DNA from lettuce and *Barnadesia* (Asteraceae): Structure, gene localization, and characterization of a large inversion. Curr. Genet. 11: 553–564.

Jones, T. R., A. G. Kluge & A. J. Wolf. 1993. When theories and methodologies clash: A phylogenetic reanalysis of the North American ambystomatid salamanders. Syst. Biol. 42: 92–102.

Jukes, T. H. & C. R. Cantor. 1969. Evolution of protein molecules. Pp. 21–132 *in* H. N. Munro (editor), Mammalian Protein Metabolism. Academic Press, New York.

Kimura, M. 1980. A simple method for estimating evolutionary rate of base substitutions through comparative studies of nucleotide sequences. J. Molec. Evol. 16: 111–120.

———. 1983. The Neutral Theory of Molecular Evolution. Cambridge Univ. Press, Cambridge.

Kluge, A. G. 1989. A concern for evidence and a phylogenetic hypothesis of relationships among *Epicrates* (Boidae, Serpentes). Syst. Zool. 38: 7 25.

——— & J. S. Farris. 1969. Quantitative phyletics and the evolution of anurans. Syst. Zool. 18: 1–32.

Kron, K. A. & M. W. Chase. 1993. Systematics of the Ericaceae, Empetraceae, Epacridaceae and re-

lated taxa based upon *rbc*L sequence data. Ann. Missouri Bot. Gard. 80: 735–741.

LAVIN, M. & M. LUCKOW. 1993. Origins and relationships of tropical North America in the context of the boreotropics hypothesis. Amer. J. Bot. 80: 1–14.

———, J. J. DOYLE & J. D. PALMER. 1990. Evolutionary significance of the loss of chloroplast-DNA inverted repeat in the Leguminosae subfamily Papilionoideae. Evolution 44: 390–402.

LES, D. H. 1988. The origin and affinities of the Ceratophyllaceae. Taxon 37: 326–345.

———, D. K. GARVIN & C. F. WIMPEE. 1991. Molecular evolutionary history of ancient aquatic angiosperms. Proc. Natl. Acad. Sci. U.S.A. 88: 10119–10123.

LOCONTE, H. & D. W. STEVENSON. 1990. Cladistics of the Spermatophyta. Brittonia 42: 197–211.

——— & ———. 1991. Cladistics of the Magnoliidae. Cladistics 7: 267–296.

MANHART, J. R. Phylogenetic analysis of green plant *rbc*L sequences. Molecular Phylogenetics and Evolution (in press).

MISHLER, B. D. 1994. Cladistic analysis of molecular and morphological data. Amer. J. Phys. Anthropol. 94: 143–156.

——— & S. P. Churchill. 1985. Transition to a land flora: Phylogenetic relationships of the green algae and bryophytes. Cladistics 1: 305–328.

———, L. A. LEWIS, M. A. BUCHHEIM, K. S. RENZAGLIA, D. J. GARBARY, C. F. DELWICHE, F. W. ZECHMAN, T. S. KANTZ & R. L. CHAPMAN. 1994. Phylogenetic relationships of the "green algae" and "bryophytes." Ann. Missouri Bot. Gard. 81: 451–483.

NEI, M. 1987. Molecular Evolutionary Genetics. Columbia Univ. Press, New York.

NELSON, G. 1993. Why crusade against consensus? A reply to Barrett, Donoghue, and Sober. Syst. Biol. 42: 215–216.

NIXON, K. C., W. L. CREPET, D. STEVENSON & E. M. FRIIS. 1994. A reevaluation of seed plant phylogeny. Ann. Missouri Bot. Gard. 81: 484–533.

NORELL, M. A. & M. J. NOVACEK. 1992. Congruence between superpositional and phylogenetic patterns: Comparing cladistic patterns with fossil records. Cladistics 8: 319–337.

OLMSTEAD, R. G. 1989. Phylogeny, phenotypic evolution, and biogeography of the *Scutellaria angustifolia* complex (Lamiaceae); inference from morphological and molecular data. Syst. Bot. 14: 320–338.

PAGE, R. D. M. 1993. Genes, organisms, and areas: The problem of multiple lineages. Syst. Biol. 42: 77–84.

PALMER, J. D., B. OSORIO & W. F. THOMPSON. 1988. Evolutionary significance of inversion in legume chloroplast DNAs. Curr. Genet. 14: 65–74.

PENNY, D., M. D. HENDY & M. A. STEEL. 1991. Testing the theory of descent. Pp. 155–193 *in* M. M. Miyamoto & J. Cracraft (editors), Phylogenetic Analysis of DNA Sequences. Oxford Univ. Press, New York.

PERUTZ, M. F. & H. LEHMAN. 1968. Molecular pathology of human haemoglobin. Nature 219: 902–909.

PLATNICK, N. I., C. E. GRISWOLD & J. A. CODDINGTON. 1991. On missing entries in cladistic analysis. Cladistics 7: 337–343.

QIU, Y.-L., M. W. CHASE, D. H. LES, H. G. HILLS & C. R. PARKS. 1993. Molecular phylogenetics of the Magnoliidae: Cladistic analyses of nucleotide sequences of the plastid gene *rbc*L. Ann. Missouri Bot. Gard. 80: 587–606.

RAUBESON, L. A. & R. K. JANSEN. 1992. Chloroplast DNA evidence on the ancient evolutionary split in vascular land plants. Science 255: 1697–1699.

RIEDL, R. 1978. Order in Living Organisms. Wiley, New York.

RODMAN, J., R. A. PRICE, K. G. KAROL, E. CONTI, K. J. SYTSMA & J. D. PALMER. 1993. Nucleotide sequences of the *rbc*L gene indicate monophyly of mustard oil plants. Ann. Missouri Bot. Gard. 80: 686–699.

SOLTIS, P. S., D. E. SOLTIS & C. J. SMILEY. 1992. An *rbc*L sequence from a Miocene *Taxodium* (bald cypress). Proc. Natl. Acad. Sci. U.S.A. 89: 449–451.

SWOFFORD, D. L. 1993. PAUP: Phylogenetic Analysis Using Parsimony, Version 3.1.1. Computer program and user's manual distributed by the Illinois Natural History Survey, Champaign, Illinois.

——— & W. P. MADDISON. 1987. Reconstructing ancestral states under Wagner parsimony. Math. Biosci. 87: 199–229.

SYTSMA, K. J., J. F. SMITH & P. E. BERRY. 1991. Biogeography and evolution of morphology, breeding systems, flavonoids, and chloroplast DNA in the four Old World species of *Fuchsia* (Onagraceae). Syst. Bot. 16: 257–269.

TAYLOR, D. W. & L. J. HICKEY. 1992. Phylogenetic evidence for the herbaceous origin of angiosperms. Pl. Syst. Evol. 180: 137–156.

TEMPLETON, A. R. 1983. Phylogenetic inference from restriction endonuclease cleavage maps with particular reference to the evolution of humans and the apes. Evolution 37: 221–244.

TROITSKY, A. V., Y. F. MELEKHOVETS, G. M. RAKHIMOVA, V. K. BOBROVA, K. M. VALIEJO-ROMAN & A. S. ANTONOV. 1991. Angiosperm origin and early stages of seed plant evolution deduced from rRNA sequence comparisons. J. Molec. Evol. 32: 253–261.

WENDEL, J. F. & V. A. ALBERT. 1992. Phylogenetics of the cotton genus (Gossypium): Character-state weighted parsimony analysis of chloroplast-DNA restriction site data and its systematic and biogeographic implications. Syst. Bot. 17: 115–143.

WILSON, M. A., B. GAUT & M. T. CLEGG. 1990. Chloroplast DNA evolves slowly in the palm family. Molec. Biol. Evol. 7: 303–314.

ZIMMER, E. A., R. K. HAMBY, M. L. ARNOLD, D. A. LEBLANC & E. C. THERIOT. 1989. Ribosomal RNA phylogenies and flowering plant evolution. Pp. 205–214 *in* B. Fernholm, K. Bremer & H. Jörnvall (editors), The Hierarchy of Life: Molecules and Morphology in Phylogenetic Analysis. Elsevier Science Publishers, Amsterdam.

APPENDIX 1 (pp. 554–562).* Inferred amino acid changes on the internal branches of a nucleotide-based cladogram (one of eight equally most-parsimonious).

This table and accompanying cladogram contain information about the functional impact of specific nucleotide changes (as reflected by alterations in amino acid identity). Following the apomorphy list format of PAUP 3.1.1 (Swofford, 1993), each internal branch of the rel-

erence tree is identified by the nodes it connects. For each node pair, optimized nucleotide changes are identified by position ("POS," i.e., the 1–1428 bases of the *rbc*L gene used), character consistency index ("*c*," each of which represents a separate contribution of the ensemble consistency of the entire tree; see Farris 1989a), the actual change inferred ("NUCΔ," with arrows following the conventions in the PAUP 3.1.1 manual; Swofford, 1993: 121), amino acid changes ("AA") that occur at this position (listed nondirectionally; see below), and their substitutional category ("SC") as determined from the PAM-250 log-odds matrix of Dayhoff et al. (1978: 352; log-odds scores of 0 and above are considered labile (L), whereas negative values are here considered nonlabile (NL); potentially nonlabile (PNL) indicates mixed-odds changes at the codon involving a given position, and synonymous changes (constant amino acid identity) are indicated by "—").

For example, a line of the following form

175 1.00 c → g R, L, A NL

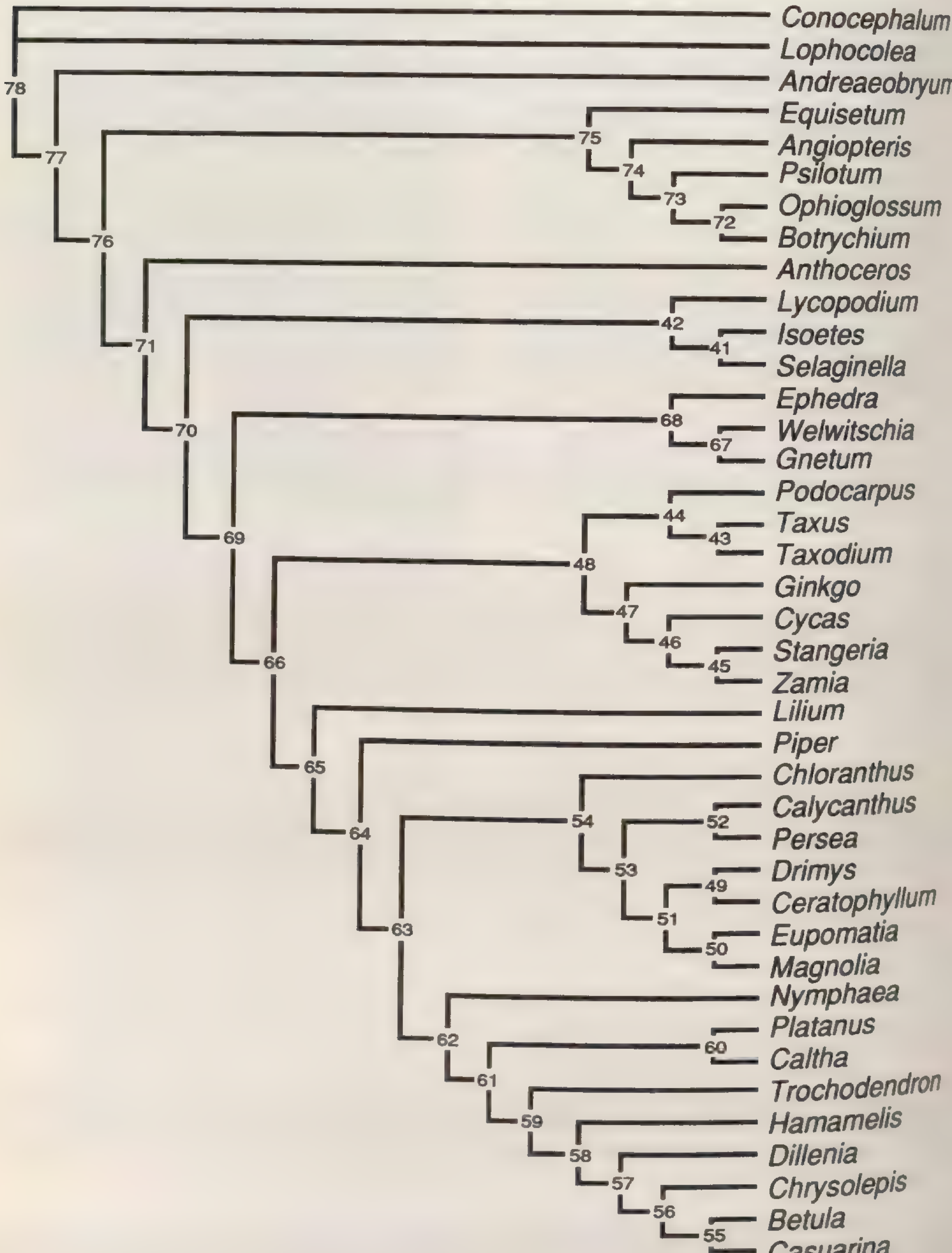
can be readily diagnosed: character 175 changes from nucleotide C to nucleotide G (on this particular tree; constancy of character-state reconstruction among all 8 trees would be indicated by a double-lined arrow) with a *c* of 1.000 (i.e., no homoplasy), and the codon in which character 175 belongs changes between the amino acids R, L, and A (using standard IUB amino acid codes; see Nei, 1987: 24; Swofford, 1993: 67). Note, however, that this does not necessarily mean that this particular character-state change gives the indicated changes in amino acid sequence; rather, it merely indicates that it *might* be involved in the changes (i.e., the C → G nucleotide transformation may not affect amino acid identify at all; thus, the indicated amino acid changes are the "worst" that can happen under the influence of character 175). The NL designation indicates that any pairwise transformation between R, L, and A would represent a nonlabile change.

In the line below

486 0.167 a → g L, S —

there is a nucleotide transformation in position 486, yet it can be positively diagnosed as *not* responsible for the different amino acid identities in its associated codon (thus, the SC is given as "—").

* Correction added in proof: P. 560, under "NODE 62 61," third line from bottom, right hand column, should read "L."


Conocephalum
Lophocolea
Andreaeobryum
Equisetum
Angiopteris
Psilotum
Ophioglossum
Botrychium
Anthoceros
Lycopodium
Isoetes
Selaginella
Ephedra
Welwitschia
Gnetum
Podocarpus
Taxus
Taxodium
Ginkgo
Cycas
Stangeria
Zamia
Lilium
Piper
Chloranthus
Calycanthus
Persea
Drimys
Ceratophyllum
Eupomatia
Magnolia
Nymphaea
Platanus
Caltha
Trochodendron
Hamamelis
Dillenia
Chrysolepis
Betula
Casuarina
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NODE 78-77

POS	c	NUCΔ	AA	SC
68	0.200	a->c	T,N	L
69	0.500	c->t	T,N	-
102	0.429	a->t	constant	-
150	0.231	a->t	A,P,S	L
165	0.231	a->t	A,W	NL
175	1.000	c->g	R,L,A	NL
186	0.222	a->c	constant	-
204	0.375	a->t	constant	-
342	1.000	a=>c	constant	-
345	0.333	t->c	constant	-
391	0.333	a=>c	R,P	L
405	0.222	t->a	constant	-
433	0.250	a->t	T,V,S,I	PNL
435	0.300	a->c	T,V,S,I	PNL
552	0.200	t=>c	constant	-
696	0.286	t=>a	constant	-
711	0.250	a->g	constant	-
740	0.667	c=>g	S,C,Y	L
764	0.400	c=>a	A,Q,E,V,H,I	PNL
767	0.333	g=>t	C,F	NL
783	0.600	t->a	constant	-
785	0.200	t->c	V,M,A	PNL
786	0.500	a->t	V,M,A	L
789	0.429	a=>t	constant	-
810	0.333	a->g	constant	-
840	0.167	a=>g	L,S	-
844	0.200	c->t	H,Y,S,F	PNL
906	0.286	a->c	D,R	-
958	0.500	t->a	L,M	L
1027	0.167	c->t	constant	-
1035	0.250	c->t	constant	-
1038	0.500	a->t	constant	-
1072	0.500	a=>c	constant	-
1095	0.500	a=>t	constant	-
1101	0.250	t->c	constant	-
1134	1.000	a->t	constant	-
1212	0.429	t=>a	constant	-
1227	0.286	t=>c	H,Q	-
1260	0.250	c->t	constant	-
1290	1.000	a=>t	constant	-
1345	0.154	g->a	A,S,T,C	L
1346	0.125	c=>g	A,S,T,C	L

NODE 77-76

POS	c	NUCΔ	AA	SC
120	0.167	t->c	constant	-
357	0.286	t->c	constant	-
426	1.000	a=>t	V,P,L,T,I	NL
567	1.000	a=>t	constant	-
660	0.167	t->c	constant	-
816	0.750	t->a	constant	-
852	0.286	c->t	constant	-
876	0.143	c->t	constant	-
927	0.231	g->t	I,M	L
930	0.111	t=>c	constant	-
960	1.000	a=>g	L,M	-
963	0.182	t->c	C,S	-
981	0.143	c->t	constant	-
984	0.182	t->c	A,S,T	-
1018	0.250	c->g	Q,E,D	L
1107	0.333	t=>a	constant	-
1111	0.286	t=>a	L,M,T	L
1113	0.500	a=>g	L,M,T	-
1116	0.222	a->t	P,A	-
1125	0.375	a->g	L,S,F,I,M	L
1137	0.231	a->g	constant	-
1176	0.250	a->g	E,D	-
1254	0.429	t=>a	constant	-
1363	0.167	c->t	constant	-

NODE 76-71

POS	c	NUCΔ	AA	SC
60	0.250	t->c	constant	-
111	0.200	a=>g	constant	-
138	0.273	t->a	P,L	-
165	0.231	t->c	A,W	-
225	0.333	t=>c	constant	-
258	0.333	t=>c	G,D,E,N,H	-
321	0.333	a=>g	constant	-
327	0.167	a->g	constant	-
351	0.167	t=>c	constant	-
486	0.167	a->g	L,S	-
564	0.214	t->a	A,V	-
603	0.143	a->g	constant	-
615	0.125	t->c	constant	-
682	0.333	t->g	S,A	L
708	0.200	a=>g	constant	-
759	0.333	a=>g	constant	-
785	0.200	c->t	V,M,A	PNL
786	0.500	t->g	V,M,A	L
844	0.200	t->c	H,Y,S,F	L
858	0.167	t=>c	constant	-
1021	0.333	g->a	V,I,L,M	-
1062	0.500	c=>t	I,Y	-
1198	0.167	t->c	L,S	-
1212	0.429	a->g	constant	-
1320	0.143	a=>g	Q,E,A	-
1335	0.167	t->c	constant	-
1398	0.250	a->g	R,K,I	-

NODE 71-70

POS	c	NUCΔ	AA	SC
88	0.143	g->a	E,K,Q,T	L
138	0.273	a->c	P,L	-
150	0.231	t=>c	A,P,S	-
153	0.111	a=>g	constant	-
261	0.167	t->c	I,L	-
315	0.167	a->g	constant	-
342	1.000	c=>t	constant	-
387	0.333	t=>c	constant	-
405	0.222	a->g	constant	-
414	0.167	a=>g	S,L	-
444	0.167	t->c	F,C	-
510	0.167	a->g	constant	-
519	0.182	c->t	constant	-
711	0.250	g->a	constant	-
720	0.200	a->g	constant	-
792	0.500	t->c	I,S	-
795	0.250	t->c	V,G	-
822	0.143	t->c	constant	-
876	0.143	t->c	constant	-
981	0.143	t->c	constant	-
1071	0.167	t=>c	constant	-
1101	0.250	c->t	constant	-
1128	0.222	t->c	constant	-
1149	0.111	t->c	constant	-
1168	0.250	t=>c	L,*	-
1170	0.143	a=>g	L,*	-
1179	0.400	t=>c	constant	-
1245	0.200	t->a	constant	-
1363	0.167	t->c	constant	-

NODE 70-42

POS	c	NUCΔ	AA	SC
48	0.500	t=>c	constant	-
102	0.429	t=>c	constant	-
109	0.333	t->c	constant	-
280	0.250	g->a	D,E,K,T	L
313	0.250	t->c	constant	-
336	0.250	t->c	constant	-
403	0.333	c=>t	constant	-
447	0.167	a->g	Q,M,I,T,L,W	L
453	0.273	a->g	constant	-
543	0.333	t->c	constant	-
597	0.167	t->c	constant	-
630	0.300	a->g	P,A	-
648	0.200	t->c	constant	-
690	0.429	t=>c	A,G,T	-
699	0.250	t->c	constant	-
711	0.250	a->t	constant	-
729	0.250	t->c	constant	-
840	0.167	g->a	L,S	-
843	1.000	t=>c	A,S	-
870	0.600	t->a	constant	-
885	0.286	t->c	constant	-
915	0.167	a->g	K,R	-
975	0.333	t=>c	constant	-
982	0.182	g->t	A,S,T	L
1005	0.375	t->c	constant	-
1018	0.250	g->c	Q,E,D	L
1042	0.167	t->c	L,S	-
1068	0.333	a->g	K,R,E	-
1077	0.200	t->c	constant	-
1176	0.250	g->a	E,D	-
1198	0.167	c->t	L,S	-
1206	0.111	t->c	constant	-
1221	0.200	a=>g	L,S	-
1236	0.333	a=>g	constant	-
1260	0.250	t->c	constant	-
1329	0.600	a=>g	D,■	-
1335	0.167	c->t	constant	-
1345	0.154	a=>t	A,S,T,C	L
1350	0.250	a->g	constant	-
1371	0.200	t->c	constant	-

NODE 42-41

POS	c	NUCΔ	AA	SC
132	0.286	t->c	constant	-
189	0.375	t=>c	constant	-
207	0.600	t=>c	constant	-
225	0.333	c=>t	constant	-
267	0.375	t=>c	P,T	-
297	0.200	t=>c	A,V,C	-
324	0.167	t=>c	constant	-
441	0.286	t=>c	constant	-
459	0.250	t=>c	constant	-
528	0.429	a->g	constant	-
567	1.000	t->c	constant	-
676	0.500	t=>a	Y,N,F	NL
696	0.286	a=>g	constant	-
702	0.200	a=>g	constant	-
718	0.333	t=>c	constant	-
744	0.250	a=>g	constant	-
768	0.167	t=>c	C,F	-
780	0.143	a=>g	constant	-
855	0.400	a=>g	constant	-
897	0.667	a=>t	A,V	-
912	0.333	a=>g	constant	-
969	0.429	a=>g	constant	-
993	0.750	a=>g	constant	-

996	0.400	a=>g	constant	-	279	0.167	a=>g	constant	-	456	0.222	t->a	constant	-					
1011	0.429	a=>g	constant	-	315	0.167	g->a	constant	-	471	0.500	t=>g	A,V	-					
1021	0.333	a->g	V,I,L,M	L	412	0.200	t=>c	S,L	-	505	0.200	c->t	constant	-					
1095	0.500	t=>c	constant	-	505	0.200	t->c	constant	-	538	0.400	t=>c	L,I	-					
1137	0.231	g->a	constant	-	534	0.200	a=>g	constant	-	718	0.333	t->c	constant	-					
1140	0.300	a=>g	constant	-	549	0.200	a->g	constant	-	759	0.333	g=>a	constant	-					
1164	0.333	t=>c	P,Q,S	-	600	0.333	t=>c	constant	-	768	0.167	t=>c	C,F	-					
1212	0.429	g->c	constant	-	624	0.667	t=>c	constant	-	825	0.375	t=>g	T,I	-					
1296	0.333	t=>c	constant	-	663	0.500	c->t	V,C	-	835	0.500	a=>t	S,I,T	L					
1377	1.000	t=>c	constant	-	687	0.167	a->g	constant	-	836	0.222	g=>c	S,I,T	L					
					696	0.286	a=>g	constant	-	837	0.300	c=>g	S,I,T	-					
NODE 70-69					780	0.143	a=>g	constant	-	1023	0.231	c->a	V,I,L,M	-					
POS	**c**	**NUCΔ**	**AA**	**SC**	813	0.231	a=>g	constant	-	1122	0.400	t=>c	constant	-					
10	0.500	c=>a	-		861	0.143	t->c	constant	-	1128	0.222	c->t	constant	-					
excluded, (PRIMER)					963	0.182	c->t	C,S	-	1198	0.167	c->t	L,S	-					
15	1.000	g=>a	-		1029	0.250	a->g	constant	-	1224	0.429	a->g	constant	-					
excluded, (PRIMER)					1047	0.429	t=>g	constant	-	1263	0.500	a=>g	R,*	-					
75	0.125	c->t	Y,F	-	1056	0.167	c->t	constant	-	1389	0.143	g->a	constant	-					
84	0.214	t=>g	D,E,Q	L	1140	0.300	a=>g	constant	-	1397	1.000	a->t	R,K,I	NL					
88	0.143	a->c	E,K,Q,T	L	1173	0.167	t=>c	constant	-	1413	1.000	a->t	T,A,S,E,P	-					
108	0.400	t=>c	I,T	-	1185	0.200	a=>g	constant	-										
124	1.000	a=>g	M,V,L	L	1203	0.200	a=>g	constant	-	**NODE 44-43**									
126	1.000	g=>a	M,V,L	-	1398	0.250	g->a	R,K,I	-	**POS**	**c**	**NUCΔ**	**AA**	**SC**					
165	0.231	c->a	A,W	-						10	0.500	a->c	- excluded,						
201	0.250	t=>c	constant	-	**NODE 66-48**					18	0.333	g->a	- excluded,						
246	0.333	t=>a	constant	-	**POS**	**c**	**NUCΔ**	**AA**	**SC**	81	0.333	t->a	constant	-					
271	0.250	g->c	P,A,V,T	L	33	0.500	t=>c	V,S,F,D,A	-	258	0.333	c=>t	G,D,E,N,H	-					
318	0.250	t=>c	constant	-	84	0.214	g=>a	D,E,Q	-	284	0.286	a=>g	N,D,S,T,E,G	L					
321	0.333	g=>t	constant	-	138	0.273	c->t	P,L	-	318	0.250	c=>t	constant	-					
327	0.167	g->a	constant	-	243	0.200	a=>g	constant	-	414	0.167	g=>a	S,L	-					
388	0.333	t=>c	constant	-	290	0.125	a->t	Y,F	L	435	0.300	c=>a	T,V,S,I	-					
397	0.333	t->c	L,S,I	-	297	0.200	t=>c	A,V,C	-	450	0.214	t=>c	constant	-					
486	0.167	g->a	L,S	-	309	0.143	t->c	constant	-	498	0.333	c->t	constant	-					
504	0.167	t->c	constant	-	312	0.182	t->c	P,F	-	504	0.167	c=>t	constant	-					
522	0.286	t->c	constant	-	346	0.333	a->c	M,L	L	507	0.333	a=>g	constant	-					
660	0.167	c->t	constant	-	498	0.333	t->c	constant	-	522	0.286	c->a	constant	-					
661	1.000	g=>t	V,C	-	546	0.250	t=>c	constant	-	564	0.214	a->c	A,V	-					
662	1.000	t=>g	V,C	-	552	0.200	c->t	constant	-	579	0.375	t=>c	constant	-					
663	0.500	a->c	V,C	-	570	0.200	t=>c	constant	-	612	0.111	g->a	constant	-					
672	0.300	t->a	constant	-	612	0.111	a->g	constant	-	618	0.333	a=>g	constant	-					
673	0.111	c=>a	L,I	-	639	0.333	t=>c	constant	-	702	0.200	a=>g	constant	-					
764	0.400	a=>t	A,Q,E,V,H,I	NL	656	0.500	t->g	L,V,C	-	813	0.231	g->a	constant	-					
786	0.500	g->t	V,M,A	-	657	1.000	a=>c	L,V,C	NL	952	0.500	t=>c	L,S	-					
810	0.333	g->a	constant	-	693	0.167	a->g	constant	-	984	0.182	c->t	A,S,T	-					
837	0.300	t->c	S,I,T	-	771	0.375	t->c	constant	-	1045	0.333	c=>t	constant	-					
852	0.286	t->c	constant	-	808	0.167	t=>c	constant	-	1107	0.333	a=>c	constant	-					
864	0.333	t=>c	constant	-	810	0.333	a->g	constant	-	1116	0.222	a=>g	P,A	-					
906	0.286	c->t	D,R	-	822	0.143	c->t	constant	-	1137	0.231	g=>a	constant	-					
927	0.231	t->g	I,M	L	885	0.286	t=>c	constant	-	1140	0.300	g=>a	constant	-					
940	0.250	t=>c	L,S	-	914	0.143	a->g	K,R	L	1215	1.000	a->c	constant	-					
1017	0.333	t=>a	constant	-	954	0.286	a=>g	L,S	-	1266	0.429	t=>c	constant	-					
1023	0.231	a=>c	V,I,L,M	-	1021	0.333	a->g	V,I,L,M	L	1338	0.333	t=>c	constant	-					
1058	0.500	a=>t	Y,F,C,L	L	1042	0.167	t=>c	L,S	-	1346	0.125	g=>c	A,S,T,C	L					
1116	0.222	t=>a	P,A	-	1221	0.200	a=>g	L,S	-	1359	0.286	c->t	P,A,L	-					
1123	0.250	t=>c	L,S,F,I,M	L	1245	0.200	a->t	constant	-										
1212	0.429	g->a	constant	-	1320	0.143	g=>a	Q,E,A	-	**NODE 48-47**									
1330	0.167	a->g	I,V	L	1332	0.500	t=>g	I,V	-	**POS**	**c**	**NUCΔ**	**AA**	**SC**					
1389	0.143	a->g	constant	-	1359	0.286	t->c	P,A,L	-	39	0.333	c=>t	constant	-					
1392	0.143	a->g	constant	-	1416	0.667	g->t	I,M,V,W	L	150	0.231	c=>t	A,P,S	-					
					1422	0.429	g->t	T,V,L,K	-	159	0.167	a=>g	constant	-					
NODE 69-66										165	0.231	a=>t	A,W	-					
POS	**c**	**NUCΔ**	**AA**	**SC**	**NODE 48-44**					549	0.200	g->a	constant	-					
90	0.250	g->a	E,K,Q,T	-	**POS**	**c**	**NUCΔ**	**AA**	**SC**	603	0.143	g->a	constant	-					
144	0.333	a->g	constant	-	90	0.250	a->g	E,K,Q,T	-	741	0.111	t->c	S,C,Y	-					
177	0.300	t=>c	R,L,A	-	147	0.154	a=>c	constant	-	861	0.143	c->t	constant	-					
264	0.333	a->g	D,E	-	264	0.333	g->a	D,E	-	906	0.286	t=>c	D,R	-					
267	0.375	t=>c	P,T	-	276	0.286	g->a	constant	-	1212	0.429	a=>g	constant	-					
276	0.286	a->g	constant	-	393	0.231	a->g	R,P	-	1269	0.600	t->c	constant	-					

1410	0.429	a->g	E,D,A,K,P,Q	-
1420	1.000	a->g	T,V,L,K	-
1421	0.667	c->t	T,V,L,K	-
1425	0.429	a->g	L,V,C	-

NODE 47-46

POS	c	NUCΔ	AA	SC
75	0.125	t=>c	Y,F	-
102	0.429	t=>c	constant	-
117	0.500	a=>g	constant	-
177	0.300	c=>t	R,L,A	-
231	0.286	t->c	constant	-
246	0.333	a=>g	constant	-
321	0.333	t=>c	constant	-
346	0.333	c->a	M,L	L
402	0.500	t->c	constant	-
405	0.222	g->a	constant	-
412	0.200	c=>t	S,L	-
519	0.182	t->c	constant	-
522	0.286	c->t	constant	-
552	0.200	t->c	constant	-
660	0.167	t=>c	constant	-
753	0.188	g->a	L,M,I	L
807	0.250	t=>c	constant	-
834	0.600	t=>c	T,M	-
957	0.400	t->a	R,C	-
963	0.182	t->c	C,S	-
1067	1.000	a=>g	K,R,E	L
1194	0.250	t=>c	S,F,A	-
1206	0.111	t=>c	constant	-
1257	0.500	t=>g	constant	-

NODE 46-45

POS	c	NUCΔ	AA	SC
88	0.143	c->a	E,K,Q,T	L
141	0.333	a=>g	constant	-
162	0.429	a=>g	A,W	-
279	0.167	g=>a	constant	-
284	0.286	a->c	N,D,S,T,E,G	L
741	0.111	c->t	S,C,Y	-
762	0.333	a=>t	A,Q,E,V,H,I	L
957	0.400	a->c	R,C	-
1209	0.286	t=>c	constant	-
1266	0.429	t=>c	constant	-
1362	0.429	a=>g	E,D	-

NODE 66-65

POS	c	NUCΔ	AA	SC
62	0.500	g=>a	R,K,T	L
66	0.167	a->g	L,I	-
88	0.143	c->g	E,K,Q,T	L
144	0.333	g->t	constant	-
153	0.111	g->a	constant	-
162	0.429	a=>g	A,W	-
168	0.273	a->g	constant	-
201	0.250	c=>a	constant	-
207	0.600	t=>g	constant	-
255	0.200	t=>c	Y,C	-
256	0.667	g=>c	G,D,E,N,H	L
271	0.250	c->g	P,A,V,T	L
363	0.250	a=>g	constant	-
378	0.500	a->c	constant	-
408	0.167	a->g	constant	-
450	0.214	t=>c	constant	-
453	0.273	a=>g	constant	-
462	0.429	t=>c	constant	-
486	0.167	a->g	L,S	-
492	0.250	a=>g	constant	-
522	0.286	c->t	constant	-
537	0.429	t->a	constant	-
579	0.375	t->c	constant	-
582	0.167	t=>c	constant	-
618	0.333	a=>g	constant	-
621	0.250	t=>c	constant	-
648	0.200	t=>c	constant	-
666	0.500	a=>c	constant	-
684	0.300	t=>g	A,S	-
690	0.429	t=>c	A,G,T	-
705	0.333	t->c	I,V	-
708	0.200	g=>a	constant	-
762	0.333	a=>c	A,Q,E,V,H,I	L
795	0.250	c->a	V,G	-
807	0.250	t=>c	constant	-
816	0.750	a=>g	constant	-
819	0.250	t=>a	constant	-
882	0.100	c->t	constant	-
912	0.333	a=>g	constant	-
933	0.143	c->t	constant	-
984	0.182	c->t	A,S,T	-
990	0.500	t->a	T,I	-
1005	0.375	t=>g	constant	-
1017	0.333	a->c	constant	-
1020	0.200	a->g	Q,E,D	-
1060	0.333	a->g	Y,F,C,L	-
1107	0.333	a=>c	constant	-
1131	0.333	a->g	constant	-
1206	0.111	t->c	constant	-
1266	0.429	t=>g	constant	-
1278	0.500	t=>g	A,V	-
1330	0.167	g->a	I,V	L
1347	0.200	t->c	A,S,T,C	-
1401	0.250	t=>c	constant	-
1407	0.500	t->c	F,I,L	-
1411	0.600	a->c	T,A,S,E,P	L

NODE 65-64

POS	c	NUCΔ	AA	SC
165	0.231	a=>t	A,W	-
186	0.222	c=>t	constant	-
228	0.125	t=>c	N,S	-
351	0.167	c=>t	constant	-
456	0.222	t->c	constant	-
537	0.429	a->g	constant	-
555	0.100	t->c	constant	-
672	0.300	a->t	constant	-
673	0.111	a=>c	L,I	L
741	0.111	t=>c	S,C,Y	-
753	0.188	g->a	L,M,I	L
879	0.667	t=>c	constant	-
915	0.167	a=>g	K,R	-
982	0.182	g=>t	A,S,T	L
990	0.500	a->c	T,I	-
1011	0.429	a=>g	constant	-
1017	0.333	c->g	constant	-
1047	0.429	g=>a	constant	-
1080	0.333	t=>c	constant	-
1137	0.231	g=>a	constant	-
1167	0.200	t=>c	A,L	-
1194	0.250	t=>c	S,F,A	-
1356	0.143	t->c	constant	-
1411	0.600	c->g	T,A,S,E,P	-
1422	0.429	g->c	T,V,L,K	-
1425	0.429	a->g	L,V,C	-

NODE 64-63

POS	c	NUCΔ	AA	SC
150	0.231	c=>t	A,P,S	-
153	0.111	a->g	constant	-
309	0.143	t=>c	constant	-
378	0.500	c->g	constant	-
474	0.250	a=>g	constant	-
564	0.214	a->g	A,V	-
612	0.111	a->g	constant	-
696	0.286	g=>a	constant	-
753	0.188	a->c	L,M,I	-
771	0.375	t=>c	constant	-
813	0.231	g->a	constant	-
885	0.286	t=>c	constant	-
927	0.231	g=>a	I,M	L
951	0.222	a->g	constant	-
1060	0.333	g->a	I,Y	-
1299	0.125	a=>g	constant	-
1320	0.143	g=>a	Q,E,A	-
1380	0.200	a=>g	E,A	-

NODE 63-54

POS	c	NUCΔ	AA	SC
84	0.214	g=>c	D,E,Q	L
433	0.250	t->a	T,V,S,I	L
546	0.250	t=>c	constant	-
672	0.300	t->c	constant	-
1020	0.200	g->c	Q,E,D	L

NODE 54-53

POS	c	NUCΔ	AA	SC
543	0.333	t=>c	constant	-
813	0.231	a->g	constant	-
982	0.182	t->g	A,S,T	L
1245	0.200	a->t	constant	-

NODE 53-51

POS	c	NUCΔ	AA	SC
45	0.750	t->c	constant	-
424	0.200	c=>a	V,P,L,T,I	L
425	0.200	c->t	V,P,L,T,I	PNL
433	0.250	a=>g	T,V,S,I	L
434	0.250	c=>t	T,V,S,I	L
672	0.300	c->t	constant	-
753	0.188	c=>g	L,M,I	L
864	0.333	c->t	constant	-
915	0.167	g->a	R,K	-
1408	0.500	g=>a	E,D,A,K,P,Q	L

NODE 51-49

POS	c	NUCΔ	AA	SC
162	0.429	g->a	constant	-
168	0.273	g->a	constant	-
655	0.250	t=>g	L,V,C	L
684	0.300	g=>a	S,A	-
732	0.125	a=>g	constant	-
836	0.222	g=>c	S,I,T	L
1131	0.333	g=>a	constant	-
1167	0.200	c=>t	A,L	-
1345	0.154	a=>t	A,S,T,C	L

NODE 51-50

POS	c	MUCΔ	AA	SC
57	0.333	t=>g	D,E	L
84	0.214	c=>a	D,E,Q	L
284	0.286	a=>g	N,D,S,T,E,G	L
561	0.333	a=>g	constant	-
774	0.500	a=>g	R,K	-
1111	0.286	a=>t	L,M,T	L
1140	0.300	g=>c	constant	-
1318	0.500	g=>c	Q,E,A	L

NODE 53-52

POS	c	MUCΔ	AA	SC
108	0.400	c=>t	I,T	-
290	0.125	a=>t	Y,F	L
297	0.200	t=>c	A,V,C	-
357	0.286	c=>t	constant	-
673	0.111	c=>a	L,I	L
682	0.333	g=>t	S,A	L
771	0.375	c=>t	constant	-
807	0.250	c=>t	constant	-
855	0.400	a=>g	constant	-
1239	0.500	t=>c	constant	-
1410	0.429	a->c	E,D,A,K,P,Q	L

NODE 63-62

POS	c	MUCΔ	AA	SC
138	0.273	c=>t	P,L	-
279	0.167	g=>a	constant	-
435	0.300	c=>t	T,V,S,I	-
456	0.222	c->t	constant	-
732	0.125	a->g	constant	-
762	0.333	c->g	constant	-
861	0.143	c=>t	constant	-
1017	0.333	g->a	constant	-
1032	0.429	t=>c	constant	-
1245	0.200	a->g	constant	-
1251	0.273	a->c	G,A	-
1266	0.429	g->a	constant	-
1270	0.500	t->c	L,S,V	-
1341	0.333	a->g	constant	-
1356	0.143	c->t	constant	-
1422	0.429	c->t	T,V,L,K	-

NODE 62-61

POS	c	MUCΔ	AA	SC
84	0.214	g=>a	D,E,Q	-
165	0.231	t->c	A,W	-
276	0.286	g=>a	constant	-
393	0.231	a=>c	R,P	-
420	0.250	t->c	I,V	-
672	0.300	t->a	constant	-
684	0.300	g=>a	S,A	-
762	0.333	g->t	constant	-
858	0.167	c=>t	constant	-
1005	0.375	g->t	constant	-
1015	0.500	c=>a	constant	-
1111	0.286	a=>c	L,M,T	-
1113	0.500	g=>a	L,M,T	-
1167	0.200	c=>t	A,L	-

NODE 61-59

POS	c	MUCΔ	AA	SC
177	0.300	c->g	R,L,A	-
290	0.125	a=>t	Y,F	L
564	0.214	g=>a	A,V	-
690	0.429	c=>t	A,G,T	-
732	0.125	g->a	constant	-
836	0.222	g->c	S,I,T	L
1278	0.500	g=>a	A,V	-
1401	0.250	c=>t	constant	-

NODE 59-58

POS	c	MUCΔ	AA	SC
153	0.111	g->a	constant	-
177	0.300	g->t	R,L,A	-
228	0.125	c=>t	N,S	-
284	0.286	a=>g	N,D,S,T,E,G	L
312	0.182	t=>c	P,F	-
390	0.667	a=>g	constant	-
450	0.214	c->t	constant	-
528	0.429	a=>t	constant	-
603	0.143	g=>a	constant	-
673	0.111	c=>a	L,I	L
711	0.250	a->g	constant	-
885	0.286	c=>t	constant	-
927	0.231	a=>g	I,M	L
982	0.182	t=>g	A,S,T	L
1137	0.231	a->g	constant	-
1320	0.143	a=>g	Q,E,A	-
1380	0.200	g->a	E,A	-

NODE 58-57

POS	c	MUCΔ	AA	SC
84	0.214	a=>c	D,E,Q	L
147	0.154	a=>g	constant	-
225	0.333	c->t	constant	-
412	0.200	c=>t	S,L	-
498	0.333	t->c	constant	-
543	0.333	t=>c	constant	-
655	0.250	t=>c	L,V,C	-
684	0.300	a=>g	S,A	-
753	0.188	c->g	L,M,I	L
836	0.222	c->g	S,I,T	L
1185	0.200	g=>a	constant	-
1224	0.429	a=>g	constant	-
1251	0.273	c->t	G,A	-

NODE 57-56

POS	c	MUCΔ	AA	SC
60	0.250	c=>t	constant	-
117	0.500	a->c	constant	-
153	0.111	a->g	constant	-
220	0.500	c->g	L,V	L
267	0.375	c->a	P,T	-
378	0.500	g=>a	constant	-
384	0.333	a=>g	constant	-
424	0.200	c->a	V,P,L,T,I	L
486	0.167	g=>a	L,S	-
501	0.333	t=>c	constant	-
510	0.167	g=>a	constant	-
537	0.429	g=>a	constant	-
552	0.200	c=>t	constant	-
588	0.400	a=>g	constant	-
621	0.250	c=>t	constant	-
813	0.231	a=>c	constant	-
864	0.333	c=>t	constant	-
963	0.182	t->c	C,S	-
1029	0.250	g=>a	constant	-
1058	0.500	t=>a	Y,F,C,L	L
1071	0.167	c=>t	constant	-
1077	0.200	t=>c	constant	-
1137	0.231	g->a	constant	-
1176	0.250	g=>a	E,D	-
1203	0.200	g=>a	constant	-
1209	0.286	t=>c	constant	-
1245	0.200	g->c	constant	-
1345	0.154	a=>g	A,S,T,C	L
1346	0.125	g=>c	A,S,T,C	L
1347	0.200	c=>t	A,S,T,C	-
1362	0.429	a=>g	E,D	-
1408	0.500	g=>c	E,D,A,K,P,Q	L
1409	0.250	a=>c	E,D,A,K,P,Q	L

NODE 56-55

POS	c	MUCΔ	AA	SC
117	0.500	c->g	constant	-
165	0.231	c->a	A,W	-
168	0.273	g=>a	constant	-
393	0.231	c=>t	R,P	-
763	0.333	g=>a	A,Q,E,V,H,I	L
1335	0.167	c=>t	constant	-

NODE 61-60

POS	c	MUCΔ	AA	SC
225	0.333	c=>t	constant	-
543	0.333	t=>c	constant	-
741	0.111	c=>t	S,C,Y	-
753	0.188	c->a	L,M,I	-
813	0.231	a->g	constant	-
1026	1.000	t=>c	constant	-
1269	0.600	t=>c	constant	-
1345	0.154	a=>t	A,S,T,C	L

NODE 69-68

POS	c	MUCΔ	AA	SC
18	0.333	g->a	- excluded,	
30	0.250	t->c	constant	-
60	0.250	c->t	constant	-
81	0.333	t->a	constant	-
93	0.400	c=>t	T,P,V	-
96	0.333	a=>g	K,L,S	-
99	0.600	t->c	D,A,E	-
147	0.154	a=>g	constant	-
186	0.222	c->t	constant	-
213	0.250	c=>t	constant	-
282	0.429	a=>c	D,E,K,T	L
306	0.375	t=>a	A,V	-
351	0.167	c=>t	constant	-
366	0.667	t=>g	constant	-
372	0.250	a->t	constant	-
393	0.231	a->c	R,P	-
402	0.500	t=>c	constant	-
424	0.200	c->a	V,P,L,T,I	L
433	0.250	t=>a	T,V,S,I	PNL
434	0.250	c=>t	T,V,S,I	PNL
435	0.300	c->a	T,V,S,I	PNL
441	0.286	t->a	constant	-
444	0.167	c->t	F,C	-
495	0.167	t->c	constant	-
498	0.333	t->a	constant	-
528	0.429	a=>t	constant	-
538	0.400	t=>c	L,I	L
603	0.143	g->a	constant	-
651	0.500	t->c	constant	-
654	0.333	c->t	constant	-
655	0.250	t=>g	L,V,C	L
657	1.000	a=>t	L,V,C	-
666	0.500	a->g	constant	-
684	0.300	t->a	S,A	-
720	0.200	g->a	constant	-
732	0.125	a->g	constant	-
753	0.188	g->a	L,M,I	L
768	0.167	t->c	C,F	-

771	0.375	t=>a	constant	-
792	0.500	c->t	I,S	-
804	0.250	c->t	constant	-
834	0.600	t->c	T,M	-
836	0.222	g=>c	S,I,T	L
858	0.167	c=>t	constant	-
865	0.167	c->t	L,P	-
942	0.200	a=>g	L,S	-
957	0.400	t->a	R,C	-
981	0.143	c->t	constant	-
1038	0.500	t=>g	constant	-
1128	0.222	c->t	constant	-
1192	1.000	t=>g	S,F,A	L
1218	0.200	t->c	constant	-
1227	0.286	c->t	H,Q	-
1245	0.200	a->c	constant	-
1251	0.273	a->c	G,A	-
1323	0.333	t->g	constant	-
1332	0.500	t=>a	I,V	-
1410	0.429	a->g	E,D,A,K,P,Q	-
1414	0.333	a->g	T,A,S,E,P	L

NODE 68-67

POS	c	NUCΔ	AA	SC
33	0.500	t=>a	V,S,F,D,A	L
40	1.000	a=>c	K,Q	L
81	0.333	a->g	constant	-
150	0.231	c=>t	A,P,S	-
207	0.600	t=>g	constant	-
255	0.200	t=>c	Y,C	-
259	1.000	a=>c	I,L	L
261	0.167	c->t	I,L	-
339	0.500	t=>g	constant	-
369	0.250	t=>c	constant	-
387	0.333	c=>t	constant	-
393	0.231	c->g	R,P	-
397	0.333	c->t	L,S,I	-
427	0.333	g=>t	A,S	-
450	0.214	t->a	constant	-
459	0.250	t=>c	constant	-
513	0.750	a->g	constant	-
543	0.333	t->a	constant	-
564	0.214	a->c	A,V	-
618	0.333	a->c	constant	-
633	0.200	t=>c	constant	-
639	0.333	t=>c	constant	-
708	0.200	g=>a	constant	-
717	0.200	c=>t	constant	-
744	0.250	a=>g	constant	-
753	0.188	a->c	L,M,I	-
822	0.143	c->t	constant	-
930	0.111	c=>t	constant	-
969	0.429	a=>g	constant	-
984	0.182	c->t	A,S,T	-
1050	0.400	t=>c	constant	-
1122	0.400	t=>c	constant	-
1176	0.250	g->a	E,D	-
1179	0.400	c=>t	constant	-
1251	0.273	c->t	G,A	-
1287	0.200	a=>g	E,Q,K	-
1302	0.286	a=>g	constant	-
1320	0.143	g=>a	Q,E,A	-
1338	0.333	t=>c	constant	-
1374	1.000	t->g	constant	-
1383	0.500	a->c	V,I	-
1411	0.600	a->t	T,A,S,E,P	L
1413	1.000	a->g	T,A,S,E,P	-
1422	0.429	g->a	T,V,L,K	-
1425	0.429	a->g	L,V,C,I	-

NODE 76-75

POS	c	NUCΔ	AA	SC
28	0.500	a->g	- excluded,	
61	1.000	a=>c	R,K,T	-
66	0.167	a=>g	L,I	-
90	0.250	g=>a	E,K,Q,T	-
189	0.375	t->c	constant	-
195	0.750	a->c	constant	-
207	0.600	t=>a	constant	-
213	0.250	c->a	constant	-
345	0.333	c->t	constant	-
375	0.333	t=>c	F,S	-
403	0.333	c=>t	constant	-
415	0.250	c=>a	constant	-
445	0.500	c->a	Q,M,I,T,L,W	L
446	0.500	a->t	Q,M,I,T,L,W	NL
459	0.250	t=>c	constant	-
600	0.333	t->c	constant	-
612	0.111	a=>g	constant	-
677	0.167	a=>t	Y,N,F	L
684	0.300	t->c	S,A	-
693	0.167	a->g	constant	-
723	0.250	t->c	constant	-
764	0.400	a=>t	A,Q,E,V,H,I	NL
765	0.429	a=>c	A,Q,E,V,H,I	L
808	0.167	t->c	constant	-
845	0.500	a->t	H,Y,S,F	L
897	0.667	a=>t	A,V	-
906	0.286	c->t	D,R	-
996	0.400	a->g	constant	-
1032	0.429	t->a	constant	-
1080	0.333	t->c	constant	-
1122	0.400	t=>a	constant	-
1123	0.250	t->c	L,S,F,I,M	NL
1140	0.300	a->t	constant	-
1236	0.333	a->t	constant	-
1275	0.333	a->g	constant	-

NODE 75-74

POS	c	NUCΔ	AA	SC
31	0.500	g->t	V,S,F,D,A	PNL
96	0.333	a=>g	K,L,S	-
108	0.400	t=>c	I,T	-
109	0.333	t=>c	constant	-
159	0.167	a->g	constant	-
195	0.750	c->g	constant	-
228	0.125	t=>c	N,S	-
261	0.167	t=>c	I,L	-
276	0.286	a->c	constant	-
315	0.167	a->g	constant	-
339	0.500	t->c	constant	-
444	0.167	t=>c	F,C	-
453	0.273	a->g	constant	-
522	0.286	t=>c	constant	-
618	0.333	a->c	constant	-
738	0.667	a->g	T,N	-
780	0.143	a->g	constant	-
786	0.500	t->a	V,M,A	-
789	0.429	t=>c	constant	-
795	0.250	t->c	V,G	-
801	0.500	t=>c	constant	-
819	0.250	t=>a	constant	-
914	0.143	a->g	K,R	L
927	0.231	t->g	I,M	L
954	0.286	a=>g	S,L	-
976	0.250	a->g	constant	-
1008	0.500	a->g	constant	-
1032	0.429	a->c	constant	-
1035	0.250	t->c	constant	-
1086	1.000	t=>c	I,V,L	-
1101	0.250	c->t	constant	-
1116	0.222	t=>g	P,A	-
1182	0.250	t->c	constant	-
1287	0.200	a->g	Q,E,K	-
1350	0.250	a=>g	constant	-
1365	0.333	a->g	constant	-
1395	1.000	c=>t	constant	-
1401	0.250	t=>c	constant	-

NODE 74-73

POS	c	NUCΔ	AA	SC
69	0.500	t=>c	N,T	-
88	0.143	g->a	E,K,Q,T	L
120	0.167	c->t	constant	-
153	0.111	a=>g	constant	-
201	0.250	t->c	constant	-
213	0.250	a->c	constant	-
225	0.333	t=>c	constant	-
243	0.200	a->g	constant	-
276	0.286	c->g	constant	-
306	0.375	t->a	A,V	-
327	0.167	a->g	constant	-
345	0.333	t->c	constant	-
351	0.167	t=>c	constant	-
387	0.333	t=>a	constant	-
390	0.667	a=>g	constant	-
391	0.333	c=>a	R,P	-
397	0.333	t->c	L,S,I	L
405	0.222	a=>g	constant	-
423	0.500	t->c	constant	-
438	0.333	a=>g	K,Q	-
447	0.167	a=>g	Q,M,I,T,L,W	L
528	0.429	a->c	constant	-
678	1.000	t=>c	Y,N,F	-
693	0.167	g->a	constant	-
708	0.200	a=>g	constant	-
738	0.667	g->t	T,N	-
772	0.500	a=>c	R,K	-
808	0.167	c->t	constant	-
846	0.333	t->c	H,Y,S,F	-
942	0.200	a=>g	L,S	-
1023	0.231	a->c	V,I,L,M	-
1027	0.167	t->c	constant	-
1056	0.167	c->t	constant	-
1065	0.333	a=>g	constant	-
1077	0.200	t=>c	constant	-
1083	0.600	t->c	constant	-
1140	0.300	t->a	constant	-
1179	0.400	t=>c	constant	-
1185	0.200	a->g	constant	-
1221	0.200	a=>g	L,S	-
1254	0.429	a->g	constant	-
1272	0.667	a=>g	L,S,V	-
1275	0.333	g->a	constant	-
1359	0.286	t=>c	P,A,L	-
1398	0.250	a->g	R,K,I	-

NODE 73-72

POS	c	NUCΔ	AA	SC
31	0.500	t->g	V,S,F,D,A	PNL
81	0.333	t=>c	constant	-
117	0.500	a->c	constant	-
132	0.286	t=>c	constant	-
144	0.333	a=>g	constant	-
148	0.333	c=>g	A,P,S	L

168	0.273	a=>g	constant	-
204	0.375	t=>c	constant	-
258	0.333	t=>a	G,D,E,N,H	L
291	0.333	t=>c	Y,F	-
306	0.375	a->g	A,V	-
313	0.250	t=>c	constant	-
315	0.167	g->a	constant	-
321	0.333	a->c	constant	-
402	0.500	t=>g	constant	-
465	0.333	c=>t	constant	-
471	0.500	t=>c	V,A	-
477	0.143	a=>g	constant	-
504	0.167	t=>c	constant	-
534	0.200	a=>g	constant	-
537	0.429	t=>a	constant	-
546	0.250	t=>c	constant	-
552	0.200	c=>t	constant	-
577	1.000	c=>t	constant	-
579	0.375	t=>a	constant	-
588	0.400	a=>g	constant	-
591	0.667	t=>c	constant	-
597	0.167	t=>c	constant	-
603	0.143	a=>g	constant	-
612	0.111	g=>a	constant	-
618	0.333	c->a	constant	-
663	0.500	a=>g	V,C	-
696	0.286	a=>g	constant	-
702	0.200	a=>g	constant	-
729	0.250	t=>c	constant	-
732	0.125	a=>g	constant	-
744	0.250	a=>g	constant	-
753	0.188	g=>a	L,M,I	L
765	0.429	c->a	C,F	-
785	0.200	c=>t	V,M,A	L
804	0.250	c=>t	constant	-
837	0.300	t=>c	S,I,T	-
840	0.167	g=>a	L,S	-
849	0.250	t=>c	constant	-
852	0.286	t=>c	constant	-
870	0.600	t=>c	constant	-
876	0.143	t=>c	constant	-
914	0.143	g->a	K,R	L
945	0.750	t=>c	constant	-
969	0.429	a=>g	constant	-
976	0.250	g->a	constant	-
1021	0.333	g=>a	V,I,L,M	L
1042	0.167	t=>c	L,S	-
1053	0.200	t=>c	constant	-
1095	0.500	t=>c	constant	-
1194	0.250	t=>c	S,F,A	-
1198	0.167	t=>c	L,S	-
1200	0.600	a->c	L,S	-
1230	0.667	t->a	constant	-
1345	0.154	a->g	A,S,T,C	L
1346	0.125	g=>c	A,S,T,C	L
1362	0.429	a->c	E,D	L
1365	0.333	g->a	constant	-
1380	0.200	a=>g	E,A	-
1392	0.143	a=>g	constant	-

APPENDIX II (pp. 562–567; corrections in proof, p. 566). Inferred amino acid changes on the internal branches of a string-based cladogram (one of 165 equally most-parsimonious), including summary statistics of the string search and the resultant matrix of apomorphic recognitions.

Similar to Appendix I, the following table and accompanying reference cladogram contain information about the functional impact of specific string changes (as reflected by alterations in amino acid identity). Interpretation is as in Appendix I with the following exceptions: (i) relative branch length (changes per given branch divided by total steps) is given, (ii) "CHAR" indicates the string character number from the matrix at the end of this appendix, (iii) "POS." still refers to nucleotide position, but, here, to the starting (3′) position of a string recognition, (iv) "STR., SEQ." indicates first the number of simulated nucleotides (i.e., string length) followed by the string itself (divided to show the codon positions of its component nucleotides), and (v) "AA-seq." shows each alternative amino acid *sequence* identified by a particular string recognition. Under the latter category, internal stop codons are indicated by *1, *2, or *3 (for TAA, TAG, and TGA, respectively), and missing nucleotide data have sometimes necessitated the indication (by "?") of missing amino acids. Again, Dayhoff et al. (1978) PAM-250 log-odds calculations were determined nondirectionally for each combination of amino acid sequences.

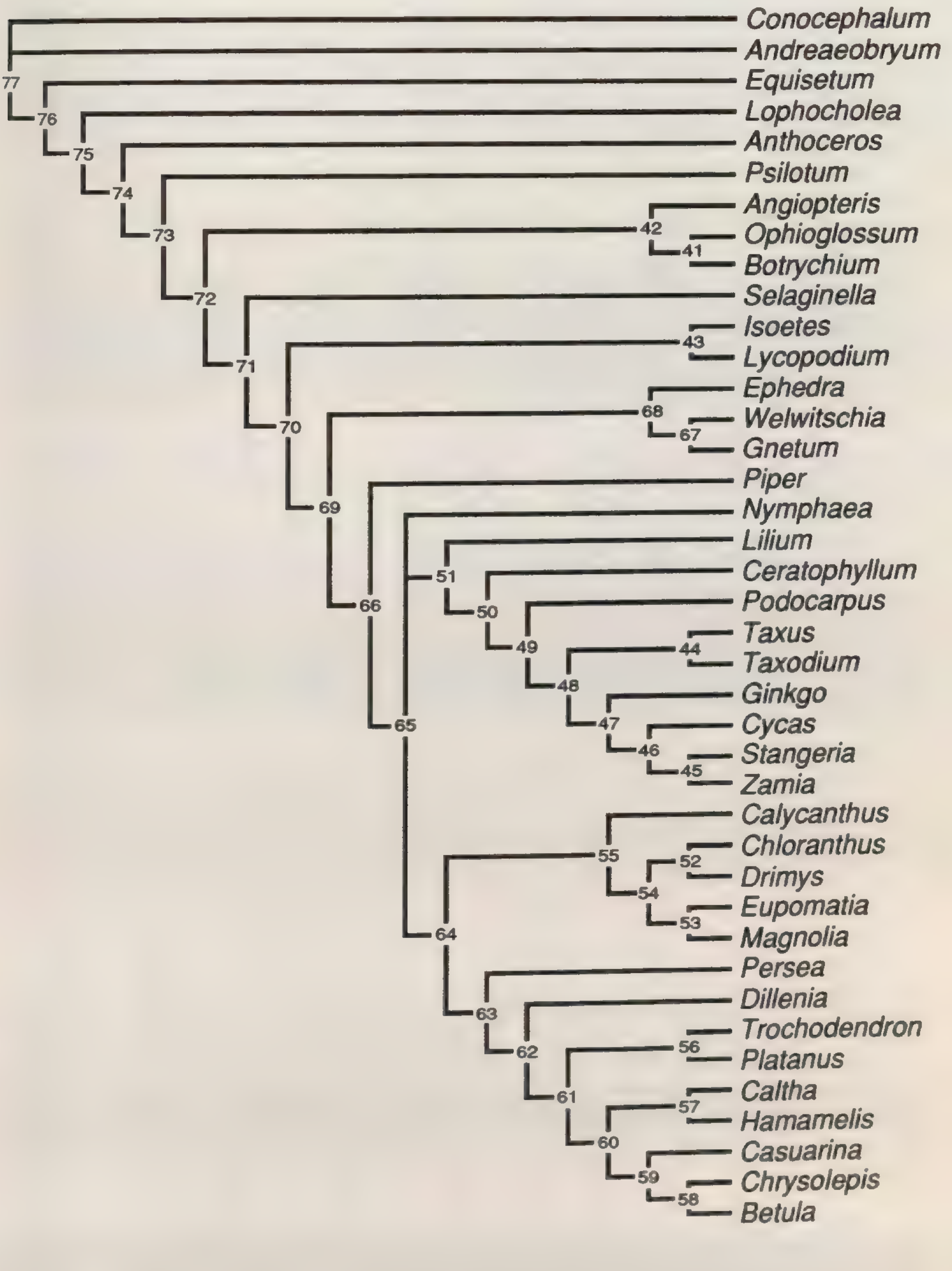
Summary statistics from the string search (involving 1000 randomly generated strings ranging in length from 6 to 21 base pairs) are provided below.

String length	Total recognitions	Total apomorphies	Total similarities	Total singletons	Total positional recognitions	Mean recognitions per string
6	758	129	77	52	47	2.745
7	204	43	20	23	31	1.387
8	107	14	10	4	13	1.077
9	5	2	1	1	2	1.000
10	4	2	1	1	2	1.000
12	21	1	1	0	1	1.000
14	5	1	1	0	1	1.000
15	8	1	1	0	1	1.000
Σ	1112	193	112	81	98	

The 1000 strings evaluated contained the following proportions of "nucleotides," which verify their random generation:

Σ A = 3375
Σ C = 3309
Σ G = 3349
Σ T = 3297

The matrix of 193 string recognitions (including 112 potentially informative similarities) is also presented. Headers are provided to give additional information for each character. The number of nucleotides per string character is given, followed by the number of recognitions (hits) per string, the start position of the string (in terms of *rbc*L nucleotides), and the character number (for reference to the table of changes). Immediately following the start position information may appear the designation "ab"; this indicates that separate string recognitions had the same start position, and so showed partial overlap (such partial correlation has been ignored in our present analyses; see text for further details). The matrix is presented in two blocks, corresponding to two rounds of string evaluation (500 strings in each, for a total of 1000). In each case, string recognitions occurring in the 3′ primer region are shown in brackets, but were ignored during parsimony analysis.


Conocephalum
Andreaeobryum
Equisetum
Lophocholea
Anthoceros
Psilotum
Angiopteris
Ophioglossum
Botrychium
Selaginella
Isoetes
Lycopodium
Ephedra
Welwitschia
Gnetum
Piper
Nymphaea
Lilium
Ceratophyllum
Podocarpus
Taxus
Taxodium
Ginkgo
Cycas
Stangeria
Zamia
Calycanthus
Chloranthus
Drimys
Eupomatia
Magnolia
Persea
Dillenia
Trochodendron
Platanus
Caltha
Hamamelis
Casuarina
Chrysolepis
Betula
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NODE 77 - 76, relative branch length = 0.0138

CHARPOS.	STR.,SEQ.	c	AA-seq.	SC
032 313b	7, tta gat t	0.500	LDL	-
091 1254	6, t gct aa	1.000	VAN, AAN	L
100 1344	6, t gct aa	0.200	AAK, ASK, ACK, ATK, RTK	PNL
136 465	6, t caa gt	0.250	IQV	-
142 607	6, gat gaa	0.125	DE	-
172 980	7, ac gct gg	0.100	HAG, HSG, HTG	L
173 1017	6, t caa gt	0.500	RQV, RDV, REV, REI, RQI, RDL	L

NODE 76 - 75, relative branch length = 0.0138

CHARPOS.	STR.,SEQ.	c	AA-seq.	SC
033 326	6, aa gaa g	0.125	EEG	-
043 487	6, aac aaa	0.143	NK	-
113 111	6, a gca gc	0.200	LAA	-
121 235	6, cgt tac	0.333	RY	-
137 728	6, ct gca g	0.167	TAG, TSG	L
152 750	6, g atg aa	0.100	MMK, MLK, MIK	L
183 1231	6, tgg gga	0.200	WG	-

NODE 75 - 74, relative branch length = 0.0138

CHARPOS.	STR.,SEQ.	c	AA-seq.	SC
035 345	6, c atg tt	0.200	NMF, NLF	L
100 1344	6, t gct aa	0.200	AAK, ASK, ACK, ATK, RTK	PNL
116 162	6, a gca gc	0.250	GAA, GWA	NL
150 724	6, gct act	0.125	AT	-
158 830	8, at act agt	0.167	NTS, NMI, NTT	PNL
166 1259	7, at cga gt	0.143	NRV, N*3V	-

NODE 74 - 73, relative branch length = 0.0079

CHARPOS.	STR.,SEQ.	c	AA-seq.	SC
018 152	6, aa gaa g	0.143	EEA	-
031 313	6, tta gat	0.500	LD	-
043 487	6, aac aaa	0.143	NK	-
092 1259	7, at cga gt	0.167	NRV	-

NODE 73 - 72, relative branch length = 0.0079

CHARPOS.	STR.,SEQ.	c	AA-seq.	SC
034 333	8, t tct gtt a	0.167	GSVT	-
085 1147	6, cat gtt	0.143	HV	-
138 500	7, gt cct tt	0.250	RPL	-
183 1231	6, tgg gga	0.200	WG	-

NODE 72 - 42, relative branch length = 0.0079

CHARPOS.	STR.,SEQ.	c	AA-seq.	SC
033 326	6, aa gaa g	0.125	EEG	-
115 155	7, aa gca gg	0.167	EAG	-
137 728	6, ct gca g	0.167	TAG, TSG	L
187 1284	6, a cag gc	0.250	VQA, VEA, VKA	L

NODE 42 - 41, relative branch length = 0.0178

CHARPOS.	STR.,SEQ.	c	AA-seq.	SC
044 543	6, t gct aa	0.143	SAK	-
052 728	6, ct gca g	0.111	TAG, TSG	L
068 939	7, a ttg gcc	1.000	VLA, VSA	NL
077 1093	8, acc caa ga	0.250	TQD, PQD	L
100 1344	6, t gct aa	0.200	AAK, ASK, ACK, ATK, RTK	PNL
113 111	6, a gca gc	0.200	LAA	-
136 465	6, t caa gt	0.250	IQV	-
142 607	6, gat gaa	0.125	DE	-
152 750	6, g atg aa	0.100	MMK, MLK, MIK	L

NODE 72 - 71, relative branch length = 0.0079

CHARPOS.	STR.,SEQ.	c	AA-seq.	SC
026 266	6, ct gtt g	0.167	PVA, PVP, PVV, TVT, SVV	PNL
053 755	7, aa aga gc	0.200	KRA	-
114 126	6, g act cc	0.500	MTP, VTP, LTP, VSP	L
193 1394	6, tc aag t	0.500	IKF, IRF, IIF	PNL

NODE 71 - 70, relative branch length = 0.0138

CHARPOS.	STR.,SEQ.	c	AA-seq.	SC
034 333	8, t tct gtt a	0.167	GSVT	-
044 543	6, t gct aa	0.143	SAK	-
052 728	6, ct gca g	0.111	TAG, TSG	L
092 1259	7, at cga gt	0.167	NRV	-
142 607	6, gat gaa	0.125	DE	-
152 750	6, g atg aa	0.100	MMK, MLK, MIK	L

NODE 70 - 43, relative branch length = 0.0099

CHARPOS.	STR.,SEQ.	c	AA-seq.	SC
006 88	6, aag acc	0.500	ET , EP, KV, DT, QT, TP	PNL
007 90	6, g acc aa	0.200	ETK, EPK, KVS, KTK, DTK, QTK, ETL, TPK, PNL	
114 126	6, g act cc	0.500	MTP, VTP, LTP, VSP	L
138 500	7, gt cct tt	0.250	RPL	-
158 830	8, at act agt	0.167	NTS, NMI, NTT	PNL

NODE 70 - 69, relative branch length = 0.0039

CHARPOS.	STR.,SEQ.	c	AA-seq.	SC
033 326	6, aa gaa g	0.125	EEG	-
183 1231	6, tgg gga	0.200	WG	-

NODE 69 - 66, relative branch length = 0.0138

CHARPOS.	STR.,SEQ.	c	AA-seq.	SC
013 141	6, a gtt cc	0.333	GVP	-
036 388	6, cta cga	0.200	LR, LP	L
043 487	6, aac aaa	0.143	NK	-
056 783	6, a gtt cc	0.250	GVP, GMP, GAP	PNL
124 273	6, t ggg ga	0.167	AGE, PGE, VGE, TGE	PNL
177 1182	6, t ggg ga	0.333	FGD	-
193 1394	6, tc aag t	0.500	IKF, IRF, IIF	PNL

NODE 66 - 65, relative branch length = 0.0079

CHARPOS.	STR.,SEQ.	c	AA-seq.	SC
010 123	12, a gta act cct ca	0.200	RVTPQ, RMTPQ, RLTPQ, RVSPQ	L
076 1067	6, aa gac c	0.200	KFR, EDR	NL
132 395	6, ct cta c	0.143	ALR, ASR, T??	NL
150 724	6, gct act	0.125	AT	-

NODE 65 - 51, relative branch length = 0.0059

CHARPOS.	STR.,SEQ.	c	AA-seq.	SC
085 1147	6, cat gtt	0.143	HV	-
152 750	6, g atg aa	0.100	MMK, MLK, MIK	L
166 1259	7, at cga gt	0.143	NRV, N*V	-

NODE 51 - 50, relative branch length = 0.0059

CHARPOS.	STR.,SEQ.	c	AA-seq.	SC
124 273	6, t ggg ga	0.167	AGE, PGE, VGE, TGE	PNL
130 386	6, ct cta c	0.167	ALR, ALP	L
142 607	6, gat gaa	0.125	DE	-

NODE 50 - 49, relative branch length = 0.0118

CHARPOS.	STR.,SEQ.	c	AA-seq.	SC
013 141	6, a gtt cc	0.333	GVP	-
035 345	6, c atg tt	0.200	NMF, NLF	L
047 635	6, tg cgt t	0.333	MRW	-
051 684	6, t cag gc	0.250	AQA, SQA, AQT, SQG	L
053 755	7, aa aga gc	0.200	KRA	-
143 639	15, c tgg aga gat cgt tt	0.500	RWRDRF	-

NODE 49 - 48, relative branch length = 0.0158

CHARPOS.	STR.,SEQ.	c	AA-seq.	SC
050 663	6, t gca ga	0.500	CAE, VAE, CAE	NL
052 728	6, ct gca g	0.111	TAG, TSG	L
085 1147	6, cat gtt	0.143	HV	-
115 155	7, aa gca gg	0.167	EAG	-
119 199	6, acc act	0.200	TT	-
130 386	6, ct cta c	0.167	ALR, ALP	L
137 728	6, ct gca g	0.167	TAG, TSG	L
166 1259	7, at cga gt	0.143	NRV, N*V	-

NODE 48 - 44, relative branch length = 0.0138

CHARPOS.	STR.,SEQ.	c	AA-seq.	SC
031 313	6, tta gat	0.500	LD	-
038 412	6, cta cga	0.333	LR, SR	NL
116 162	6, a gca gc	0.250	GAA, GWA	NL
138 500	7, gt cct tt	0.250	RPL	-
142 607	6, gat gaa	0.125	DE	-
172 980	7, ac gct gg	0.100	HAG, HSG, HTG	L

NODE 48 - 47, relative branch length = 0.0079

CHARPOS.	STR.,SEQ.	c	AA-seq.	SC
017 164	6, ct gca g	0.167	AAV, WAV	NL
053 755	7, aa aga gc	0.200	KRA	-
054 766	7, ttt gcc a	0.250	FAR, CAR, CAK	PNL
124 273	6, t ggg ga	0.167	AGE, PGE, VGE, TGE	PNL

NODE 47 - 46, relative branch length = 0.0158

CHARPOS.	STR.,SEQ.	c	AA-seq.	SC
002 54	14, a gat tac aga tta	0.200	KDYRL, RDYRL, KDYKL, KDYTI, KEYKL	PNL
024 227	6, gt ctc g	0.250	SLD, NLD	L
035 345	6, c atg tt	0.200	NMF, NLF	L
043 487	6, aac aaa	0.143	NK	-
049 655	6, tgc ttc	1.000	CF, LF, VF	NL
076 1067	6, aa gac c	0.200	KFR, EDR	NL
092 1259	7, at cga gt	0.167	NRV	-
152 750	6, g atg aa	0.100	MMK, MLK, MIK	L

NODE 46 - 45, relative branch length = 0.0059

CHARPOS.	STR.,SEQ.	c	AA-seq.	SC
012 140	7, gg gtg cc	0.333	GVP	-
132 395	6, ct cta c	0.143	ALR, ASR, T??	NL
1821207b	6, ggc ggg	0.500	GG	-

NODE 65 - 64, relative branch length = 0.0079

CHARPOS.	STR.,SEQ.	c	AA-seq.	SC
052 728	6, ct gca g	0.111	TAG, TSG	L
142 607	6, gat gaa	0.125	DE	-
168 950	6, cg tta c	0.250	ALR, ASC	NL
172 980	7, ac gct gg	0.100	HAG, HSG, HTG	L

NODE 64 - 55, relative branch length = 0.0059

CHARPOS.	STR.,SEQ.	c	AA-seq.	SC
061 856	6, gac aac	0.200	DN	-
106 1418	6, at acc t	0.500	DTL, DVL, DTV, ILC, DKL	NL
191 1355	8, gc cct gaa	0.500	SPE, SPD, SAE, SLE	L

NODE 55 - 54, relative branch length = 0.0039

CHARPOS.	STR.,SEQ.	c	AA-seq.	SC
054 766	7, ttt gcc a	0.250	FAR, CAR, CAK	NL
152 750	6, g atg aa	0.100	MMK, MLK, MIK	L

NODE 54 - 52, relative branch length = 0.0020

CHARPOS.	STR.,SEQ.	c	AA-seq.	SC
021 198	6, g aca ac	0.250	WTT	-

NODE 54 - 53, relative branch length = 0.0059

CHARPOS.	STR.,SEQ.	c	AA-seq.	SC
073 1135	6, tca ggc	0.500	SG	-
079 1110	7, t ttg cca	1.000	SLP, STP, SLA, SMP	NL
176 1138	6, ggc ggt	0.500	GG	-

NODE 64 - 63, relative branch length = 0.0020

CHARPOS.	STR.,SEQ.	c	AA-seq.	SC
192 1369	7, gct gct t	0.167	AAC	-

NODE 63 - 62, relative branch length = 0.0079

CHARPOS.	STR.,SEQ.	c	AA-seq.	SC
003 74	9, at acg cct g	0.200	YTPE, FTPD, YTPQ, YTPD	L
054 766	7, ttt gcc a	0.250	FAR, CAR, CAK	NL
092 1259	7, at cga gt	0.167	NRV	-
124 273	6, t ggg ga	0.167	AGE, PGE, VGE, TGE	PNL

NODE 62 - 61, relative branch length = 0.0039

CHARPOS.	STR.,SEQ.	c	AA-seq.	SC
098 1338	6, t gag gc	0.333	REA, EEA	NL
175 1109	6, ct cta c	0.333	SLP, STP, SLA, SMP	NL

NODE 61 - 56, relative branch length = 0.0039

CHARPOS.	STR.,SEQ.	c	AA-seq.	SC
015 146	8, ca cct gag	0.100	PPE, PAE, PSE	PNL
145 684	6, a cag gc	0.333	AQA, SQA, SQG, AQT	L

NODE 60 - 57, relative branch length = 0.0039

CHARPOS.	STR.,SEQ.	c	AA-seq.	SC
018 152	6, aa gaa g	0.143	EEA	-
090 1245	7, g ggt gcc	0.500	PGA, PGG, PVA, PGR, PRA	NL

NODE 60 - 59, relative branch length = 0.0099

CHARPOS.	STR.,SEQ.	c	AA-seq.	SC
076 1067	6, aa gac c	0.200	KFR, EDR	NL
100 1344	6, t GCT aa	0.200	AAK, ASK, ACK, ATK, RTK	PNL
137 728	6, ct gca g	0.167	TAG, TSG	L
152 750	6, g atg aa	0.100	MMK, MLK, MIK	L
177 1182	6, t ggg ga	0.333	FGD	-

NODE 59 - 58, relative branch length = 0.0039

CHARPOS.	STR.,SEQ.	c	AA-seq.	SC
139 501	6, c ccc ct	1.000	RPL	-
146 686	9, ag gct gaa a	0.333	QAET, QGET, QTET	L

NODE 69 - 68, relative branch length = 0.0079

CHARPOS.	STR.,SEQ.	c	AA-seq.	SC
027 267	6, t gtt cc	0.250	PVP, PLP, PVV, TVT, SVV, PVA	PNL
029 543	6, t gct aa	1.000	SAK	-
137 728	6, ct gca g	0.167	TAG, TSG	L
166 1259	7, at cga gt	0.143	NRV, N*V	-

NODE 68 - 67, relative branch length = 0.0197

CHARPOS.	STR.,SEQ.	c	AA-seq.	SC
025 252	6, c tac ga	0.250	CYD, CYG, CYE, CYN, CYH	PNL
034 333	8, t tct gtt a	0.167	GSVT	-
047 635	6, tg cgt t	0.333	MRW	-
076 1067	6, aa gac c	0.200	KFR, EDR	NL
092 1259	7, at cga gt	0.167	NRV	-
116 162	6, a gca gc	0.250	GAA, GWA	NL
130 386	6, ct cta c	0.167	ALR, ALP	L
150 724	6, gct act	0.125	AT	-
170 966	6, t ggg ga	0.333	GGD	-
192 1369	7, gct gct t	0.167	AAC	C

Corrections in proof: P. 564, under "NODE 70–43," fourth line from bottom, delete comma after "TPK" and move "PNL" to right hand column; p. 566, under "NODE 68–67," bottom line, right hand column, should read " ."

@nucl./string	76	8197666761	6767886666	6776666616	6768666666	6666676666	6677667866	6667667767	6678668677	6676668767	6776676676	6667666
	--	-4--------2	----------	--------0-	----------	----------	----------	----------	----------	----------	----------	-------
Σhits/string	78	3514228272	3743113438	1225216438	9443422241	1212213138	9312242122	1391122232	4131425322	7123412217	2223312822	2294871
	--	3---56---1	--2-1-505	7-0-58-0--	--0143-528	-8745-0-0-	-52042---4	70--7---0-	48--06--00	-8-047--8-	40-00-----4	-------
String start	00	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0011111111	1111111111	1111111
position	00	0000000011	1111111111	2222222222	3333333444	4445556666	6777777888	8899999999	9910000011	1111122222	2222222333	3333444
	01	4578889902	3444466577	9112566788	1123489112	2384673556	8256688344	5600011356	7834669912	2233422244	5566689344	7999011
	48	9441480643	6015604234	8257267803	3363582272	5673735253	4856835319	6925703934	2950473502	3711735545	4936663814	8044789
	--	---------	---------	---------	ab-------	---------	---------	---------	---------	--ab--ab--	---ab-----	--ab---
Character #	XX	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000001	1111111
	XX	0000000001	1111111112	2222222223	3333333334	4444444445	5555555556	6666666667	7777777778	8888888889	9999999990	0000000
	XX	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567
Conocephalum	[??]	??0000000000	0000000100	0000001000	1110000000	0011001000	0110000001	0000000000	0100000000	0000100000	1000000000	0??????
Lophocolea	[??]	?011000000	1001000100	0000010000	1001000000	0001002???	0110000000	0010000000	?00?000000	0000100010	0000000001	0??????
Anthoceros	[??]	???0001000	0100000100	0000110000	1101100000	0000??????	?100000000	0000000000	0?0?000000	0000100000	0000000000	0??????
Andreaeobryum	[??]	??00011000	0000001011	1000110000	1111000?00	0011001000	0110000000	0000000000	0010000000	0000100000	1000000100	???????
Ophioglossum	[10]	1000000000	0000000000	0001010100	0010100000	0010001000	0010000000	0000000100	0000001000	0000000100	0100000001	0011???
Psilotum	[10]	0000000000	0000101000	0000010000	0001100000	0111001000	0110000010	0000000000	0000000000	0101100000	0100100000	0000???
Isoetes	[?0]	1100011000	0000100000	0000000000	0001100000	1010001000	0000000000	0000001000	0000011000	0000001000	0001000000	0000???
Lycopodium	[10]	0000011100	0000000000	0001010000	0000000000	0010001000	0000100000	0100000000	0000000000	0000000000	0000000000	0000???
Angiopteris	[10]	1001000000	0000001100	0100010000	0010000000	0001001000	0110001000	0000110000	1000000000	0000000000	0101000000	0000???
Equisetum	[11]	1000000000	0000000100	0100010000	1011001000	0011001000	0110000000	0000000000	0100000000	0000000000	0000000001	0000???
Selaginella	[00]	1100100000	0000000000	0000000001	0000100000	0111101000	1100000000	0000000000	0000000100	0010000000	0100011000	0000???
Botrychium	[10]	1000000000	0000000000	0000001000	0000100000	0010001000	0010000111	0000000100	0000001000	0000101000	0100000001	0000???
Taxus	[??]	1?00001000	0000000000	0000000000	10?0010100	0010000001	1110010000	1000000000	0000010000	0000000000	0000000000	???????
Taxodium	[10]	1000000001	0010000100	0000000000	1011000100	0000000001	1110010000	0000000000	0000010000	0000000000	0000000000	???????
Podocarpus	[00]	1100001001	0100000000	0000001000	0011000000	0000000000	1010010000	1000000000	0000010000	1000100000	0000000000	0000000
Ginkgo	[??]	1000000001	0000101000	0000000000	0001010000	0000000101	0101010000	0000000000	0000010000	0000000000	0070000000	???????
Cycas	[??]	1100000001	0000001000	0001000000	0011110010	0010000011	1101000000	0000000000	0000001000	0000000000	0100000000	0000100
Stangeria	[??]	1100000000	0100101000	0001000000	0011100000	0010000011	0101010000	0000000000	0000000000	0000000000	0100000000	0000000
Zamia	[??]	1000000001	0100001000	0000000000	0011110000	0010010011	1001010000	0000000000	1000000000	0000000000	0100000000	0000000
Ephedra	[??]	1000000001	0001000000	0000001010	0011100000	0011001000	0010000000	0000000000	0000000000	0101000000	0000000000	0000001
Welwitschia	[00]	1000000000	0000000000	0010101010	0010101000	0010000001	0000010000	0000000000	0000010000	0000000000	0100000000	0000000
Gnetum	[??]	1000000000	0000000000	0000101010	0000100000	0010000000	0100000000	0000000010	0000011000	0000100000	0100000000	0000000
Chloranthus	[??]	1000000000	0010100000	1000000000	0011110000	0000001000	0101010000	1000000000	0000010000	0000000000	0000000000	???????
Piper	[??]	1001000000	0010001100	1000000000	0011110100	0000000000	0000010000	1000000000	1000000001	0000000000	0000000001	0000010
Drimys	[??]	1000000001	0010000000	1000010000	0011110000	0000001000	0001010000	1000000000	0000010000	0000000000	0000000000	0000010
Calycanthus	[??]	1000000001	0010000000	0000000000	0011110000	0000001000	0100010000	1000000000	0000010000	0000000000	0000000000	0000010
Eupomatia	[??]	1000000001	0010000000	0000000000	0001110001	0000001000	0101010000	1000000000	0010010010	0000000000	0000000000	0000010
Magnolia	[00]	1000000001	0010100000	0000000000	0011110000	0000001000	0101010000	1000000000	0010010010	0000000000	0010000000	0000010
Persea	[00]	1000000001	0010100000	0000000000	0011110000	0000001000	0100010000	0000000000	0000010000	0000010000	0000000010	0000000
Trochodendron	[??]	1000000001	1010100000	0000000000	0011100100	0001001000	0101010000	0000000000	0000110000	0000000001	0100000100	0000000
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Lilium	[??]	1000000001	0010000000	0000000000	0011110000	0000001000	0000010000	1000000001	0000010000	0000100000	0100000000	0100000
Platanus	[??]	1000000001	0010100000	0000000000	0011100000	0000001000	0001010000	0000000000	0000010000	0000000000	0100000000	0000000
Caltha	[??]	1000000011	0010000100	0000000000	0011100001	0000001000	0001000000	0000000000	0000010000	0001000001	0100000100	0000000
Dillenia	[??]	1000000001	0010000100	0000000000	0011100000	0000001000	0101010000	0000000000	0000010000	0000000000	0100000000	1000000
Chrysolepis	[??]	1000000001	0011000000	0010000000	0001100000	0000001000	0101010000	0001000000	0000000000	0000000000	0100000101	0000000
Betula	[??]	1000000001	0010000000	0000000000	0011100000	0010001000	0101010000	0000000000	0000000000	0000000000	0100000101	0000000
Casuarina	[??]	1000000001	0010110000	0000000000	0011100000	0001001000	0101010000	0000000000	0000000000	0000100000	0100000101	0000000
Hamamelis	[??]	1000000001	0010000100	0000000000	0011100000	0001001000	0101010000	0000000000	0000010000	0000000001	0100000100	0000000

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	387	3---	-2913908--	9---10---918	98---482-0	04---7-7---2	-4099-70---	-2---70-9-1	-54-801----	0-1-9-7-92	-94
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	222	467	8912566891	4457800368	9911268004	6038889922	2555661333	5678013566	7817038889	0033558244	569
	335	146	7716525399	5943049626	5529156017	1790464524	9099071022	8404537046	8079982495	7715144512	594
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Eupomatia	[?00]	000	0000100000	1001000001	0100000000	0000000011	0100000100	0000000100	0100011000	0010000000	110
Magnolia	[000]	000	0000100000	1001000000	0100000000	1000000001	0100000000	1000010000	0000011000	0010000000	110
Persea	[000]	000	0000100000	1001000001	0100000000	0001000001	0000000000	0000000100	0100001000	0011000000	000
Trochodendron	[?00]	000	0010100000	1000000000	0100000000	0000100001	0000000000	0000000100	0000101000	0010001000	010
Ceratophyllum	[000]	000	0000100000	1000000001	0000000000	0000100001	0100000000	0000010000	0000001000	0010000000	010
Nymphaea	[000]	000	0100100000	1001000000	0100000000	0100000001	0010000000	0000000000	0000001001	0070000000	???
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Casuarina	[?00]	000	0000100000	1000000000	0100001000	0100000001	0100000100	0000000100	0100100000	0010000000	000
Hamamelis	[?00]	000	0000100000	1000000000	0100000000	0100000001	0010000000	0000000100	0100001000	0010000000	000

Statistical Summary of Some of the Activities in the Missouri Botanical Garden Herbarium, 1993

	Vascular	Bryophyte	Total
Acquisition of Specimens			
Staff Collections (includes bryophytes)	27,402	—	27,402
Purchase	16	0	16
Exchange	53,377	2,728	56,105
Gifts	9,712	4,781	14,493
Total acquisitions	90,507	7,509	98,016
Mountings			
Newly mounted	142,737	21,558	164,295
Mounted when received	15,994	0	15,994
Total specimens filed	158,731	21,558	180,289
Repairs			
Specimens repaired	36,885	n/a	36,885
Specimens stamped	4,858	n/a	4,858
Total repairs	41,743	0	41,743
Specimens sent			
On exchange	31,807	7,433	39,240
As gifts	23,535	3,656	27,191
Total	55,342	11,089	66,431
Loans sent			
Total transactions	741	32	773
Total specimens	30,309	2,426	32,735
To U.S. institutions			
Transactions	397	23	420
Specimens	15,576	931	16,507
To foreign institutions			
Transactions	433	9	442
Specimens	14,733	1,495	16,228
To student investigators			
Transactions	65	8	73
Specimens	7,670	485	8,155
To professional investigators			
Transactions	676	24	700
Specimens	22,639	1,941	24,580
Loans received			
Transactions	446	14	460
Specimens	32,097	2,500	34,597

	From U.S.	From abroad	Total
Visitors	412	131	543

On 31 December 1993 the total number of mounted, accessioned specimens in the herbarium was 4,292,346 (4,050,977 vascular plants and 241,469 bryophytes).—David Brunner, *Curator of the Herbarium.*

NOTICE

The Rupert Barneby Award

The New York Botanical Garden is pleased to announce that Dr. André Mauricio de Carvalho, of the Centro de Pesquisas do Cacau, Itabuna, Brasil, and Prof. Ricardo Vanni, of the Instituto de Botánica del Nordeste, Corrientes, Argentina, are the recipients of the 1993 Rupert Barneby Award. Dr. Carvalho will use his award to continue his work on a taxonomic treatment of New World *Dalbergia*. Prof. Vanni will be able to further his studies of *Zornia* sect. *Anisophylla* in South America, and *Stylosanthes* for the floras of Argentina and Paraguay.

The New York Botanical Garden also invites applications for the 1994 Rupert Barneby Award. The award of $1,000.00 is to assist researchers planning to come to The New York Botanical Garden to study the rich collection of Leguminosae. Anyone interested in applying for the award should submit their curriculum vitae, a letter describing the project for which the award is sought, and how the collection at NYBG will benefit their research. Travel to NYBG should be planned between January 1, 1995 and January 31, 1996. The letter should be addressed to Dr. Enrique Forero, Director, Institute of Systematic Botany, The New York Botanical Garden, Bronx, NY 10458-5126, USA, and received no later than December 2, 1994. Announcement of the recipient will be made by December 16th. Anyone interested in making a contribution to The Rupert Barneby Fund in Legume Systematics, which supports this award, may send their check, payable to The New York Botanical Garden, to Dr. Forero.

Volume 81, Number 3, pp. 403–570 of the Annals of the Missouri Botanical Garden
was published on August 1, 1994.

Two Important New Titles from the Missouri Botanical Garden

Moss Flora of Central America
Part 1. Sphagnaceae–Calymperaceae

Bruce Allen with contributions from H. Crum, R. A. Pursell, W. D. Reese, N. Salazar Allen

Central America possesses one of the world's richest moss floras, with an estimated 871 species in an area only one-half that of Colombia, which has about as many species. Previous to this publication the only moss flora for any Central American country was E. B. Bartram's now nearly half-century old *Mosses of Guatemala*.

The *Moss Flora of Central America* is based on historic and extensive recently collected material from the area, with each species fully described and discussed with its distribution in Central America mapped on an individual map. Families and genera are fully described, and all taxa are keyed. Extensive synonymy is given with types cited for all names. The *Flora* will appear in four parts during the next few years. Part 1 constitutes Monographs in Systematic Botany from the Missouri Botanical Garden, volume 49. 242 pages. April 1994.

Index of Mosses

Marshall R. Crosby & Robert E. Magill

Index of Mosses is a guide to the names published for mosses, including all new taxa from the rank of genus and below. Entries include full references to places of publication, and, depending on the nature of the name, listings of basionyms, replaced names, and types. The *Index of Mosses, 1963–1989*, lists about 8500 names and contains appendices giving full authors' names and fully spelled journal and book titles with references to their entries in *TL-2* and *B-P-H*. *Index of Mosses, 1990–1992*, contains about 800 names and a bibliography of the publication in which nova for 1990–1992 appeared. Monographs in Systematic Botany from the Missouri Botanical Garden, volume 42 (1992) and 50 (May 1994), 656 and 87 pages respectively.

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Cover illustration. *Petrea sulphurea* M. J. Jansen-Jacobs, by Phyllis Bick.

Annals of the Missouri Botanical Garden 1994

Volume 81
Number 4

Volume 81, Number 4
Fall 1994

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Missouri Botanical Garden

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The mission of the Missouri Botanical Garden is to discover and share knowledge about plants and their environment, in order to preserve and enrich life.

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REVISION OF *HILLIA* (RUBIACEAE)[1]

Charlotte M. Taylor[2]

Abstract

Hillia Jacq. is a genus of 24 usually epiphytic species that are distinguished by their convolute corolla aestivation and comose seeds. Based on corolla characters, five subgenera are recognized here: subgenus *Hillia* (six species), subgenus *Andinae* C. M. Taylor (one species), subgenus *Tetrandrae* C. M. Taylor (five species), subgenus *Illustres* C. M. Taylor (seven species), and subgenus *Ravnia* (Oersted) C. M. Taylor (five species). Keys to all species of the genus are provided, and those of the first four subgenera are described and illustrated.

Hillia Jacq. is a genus of 24 species of usually epiphytic shrubs distributed widely in the moist and wet Neotropics. These species are easily separated from all other Rubiaceae by their seeds with a tuft of "trichomes" 1–3 cm long attached at one end, and can usually also be recognized by a succulent epiphytic habit, caducous ligulate stipules that are interpetiolarly connate, solitary flowers, and cylindrical woody capsules. The corollas may have one of several combinations of color and form: white and salverform, green to yellow-green or red and funnelform, or red and tubular to inflated.

Species of *Hillia* can be confused with those of *Cosmibuena* Ruiz & Pav., which are succulent epiphytes with a similar geographic range, similar capsules, and salverform white corollas similar to those of some species of *Hillia* (Taylor, 1992). *Cosmibuena* can be distinguished by its glabrous seeds, interpetiolarly and partially intrapetiolarly connate stipules, and usually three or more flowers per inflorescence. Steyermark (1974) also distinguished *Hillia* by the lack of marginal wings on the seeds; however, many seeds of *Hillia* have at least a thin marginal wing, while the seeds of *Cosmibuena* are variable in this regard. These genera can usually also be separated by their stigmas, which are bilobed, densely papillose, and held above the anthers in *Cosmibuena*, in contrast to subcap-

[1] I thank the curators of the following institutions, who kindly made specimens available: A, AAU, CAS, COL, CORD, CR, CTES, CUVC, DUKE, F, G, GB, HAC, HAJB, HUA, JBSD, MO, NY, P, UCR, UPR, UPRRP, US, VALLE, and WIS. I also thank the Department of Biology and the Fondo Institucional Para la Investigación of the University of Puerto Rico-Recinto de Río Piedras, the Manual to the Plants of Costa Rica project of the Missouri Botanical Garden, the National Science Foundation (BSR 87-00068), and the Dee Scholarship Fund of the Field Museum of Natural History for support for travel. I am indebted to colleagues who contributed through discussions and comments, notably W. Burger, D. Lorence, J. Dwyer, L. Andersson, M. H. Grayum, W. Haber, B. Hammel, W. D. Stevens, R. Thomas, D. J. Lodge, and E. Christensen. I thank R. E. Gereau, Z. Mercado, T. Zanoni, B. Molano, P. Hoch, P. Berry, and J. Pipoly for help with analyses, exsiccatae records and fieldwork.

[2] Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166-0299, U.S.A.

itate to bilobed or linear, less densely papillose, and sometimes held below the anthers in *Hillia*. Other characters used to separate these genera by previous authors were discussed by Taylor (1992).

Hillia was published with the single species *H. parasitica* Jacq., the most widespread and common species in the genus, which he described from the Antilles. The name commemorates Sir John Hill (1716–1775), a "pompous" (Smith, 1814) British apothecary and "author of several voluminous but useless botanical works" (Sims, 1804), and it has been suggested that the specific epithet was intended as much to describe Hill's botanical work as the plant's habit. *Hillia* has not been treated comprehensively since de Candolle (1830) recognized three species. Reviews of its characteristics, relationships, and notable species were presented by Bentham & Hooker (1873), Schumann (1889, 1891), and Steyermark (1963, 1972). Descriptions of individual species or local groups of species may be found in various regional treatments covering areas from southern Mexico and the Antilles through Peru, Bolivia, and southern Brazil.

Saldanha Vell. was first combined with *Hillia* by Schumann (1889), who included species with both salverform white corollas and funnelform green corollas in this genus. However, the variation in corolla form encompassed within the genus has not been recognized by all authors, particularly those working in Central America where representatives of subgenus *Illustres* C. M. Taylor were unknown until recently. Based on a survey of this variation, the Central American genus *Ravnia* Oerst. was recently reduced to a subgenus of *Hillia* (Taylor, 1989). In spite of the considerable variation in corolla form, subgenus *Ravnia* (Oerst.) C. M. Taylor was the first subgenus published in *Hillia*. In the present treatment I recognize five subgenera: subgenus *Hillia* (six species), subgenus *Andinae* C. M. Taylor (one species), subgenus *Tetrandrae* C. M. Taylor (five species), subgenus *Illustres* (seven species), and subgenus *Ravnia* (five species).

Species of subgenus *Hillia* are found through most of the range of the genus, with the exception of Central America and Mexico. *Hillia parasitica* is found throughout the range of this subgenus; the remaining species are found from northern to central South America. In contrast, species of subgenus *Tetrandrae* are primarily found in the Greater Antilles and Central America, with one extending southward along the northwestern coast of South America. Species of subgenus *Illustres* are found in South America, with one extending north to Costa Rica. Several species of subgenus *Illustres* show wide geographical disjunctions, suggesting that they are uncommon or that the epiphytic flora of this region is poorly collected. Species of subgenus *Ravnia* are found in southern Central America, with two recently described species extending the range of this subgenus to southern Mexico and Venezuela (Taylor, 1991).

Morphology

The morphology of subgenus *Ravnia* has been described previously (Taylor, 1989). The discussion presented here applies to the species of *Hillia* including those of subgenus *Ravnia*.

Habit, Stems, and Vestiture

Plants of *Hillia* are erect or sometimes clambering succulent shrubs, small trees, or lianas; habit is variable in most species. They are usually epiphytes but may also be terrestrial or rheophytic (*H. rivalis* C. M. Taylor). *Hillia parasitica* is frequently rooted in soil, although in Puerto Rico this species is found rooted only on wet mountaintops where the soil is saturated throughout the year (Ewel & Whitmore, 1972) and root growth of most plants is limited. The branches of most species are elongate, to a meter or more in length, and flexuous. The stems may be quadrate when young, but usually become rounded with age. The bark is usually smooth and grayish brown, but may be deep reddish brown in occasional individuals of some species. Such reddened bark appears to be correlated with reddened stipules and corollas that are flushed with pink in individual plants. The bark of *H. killipii* Standley has a distinctive coppery red color and thin papery texture, and is usually wrinkled or circumferentially ridged, particularly on young twigs. Plants of all species are glabrous throughout. Raphides are found in all parts, but are particularly evident in the stipules, ovaries, and abaxial surface of the leaf veins.

Leaves

The leaves are isophyllous (or anisophyllous in some plants of *Hillia triflora* (Oerst.) C. M. Taylor) and petiolate (or subsessile in *H. costanensis* Steyerm.), although the blades may be attenuate at the base and the petiole difficult to delimit precisely. The blades are succulent, entire, and generally elliptic to oblanceolate or lanceolate. The secondary veins are pinnate with at least one pair of veins arising distally to the middle of the blade, or subpalmate in *H. ulei* K. Schum. and *H. oaxacana* C. M. Taylor, with all of the veins arising proximally

to the middle of the blade. The veins are usually plane, or the secondary veins may be prominulous to prominent abaxially in some species of subgenus *Hillia*, and the higher order venation is characteristically prominulous as well in *H. bonoi* Steyerm. In most species the venation is indistinct due to the succulence of the leaves. Domatia are generally lacking, although occasional crypt or pocket domatia are found in *H. bonoi* and *H. macrophylla* Standl.

The stipules are interpetiolar, ligulate to oblanceolate, and caducous. They are finely veined in a subparallel, subpalmate pattern. They become pale green to white before falling, or red in some individuals of some species. The flowering nodes are usually subtended by stipules that are similar in shape and size to those of vegetative nodes; these stipules are also usually caducous, but in some individuals of some species they persist until anthesis. Such persistent stipules have been called "bracts" by some authors (e.g., Steyermark, 1972, 1974). These structures are here called "stipules subtending flowers."

FLOWERS

The flowers are terminal and solitary, infrequently three in *H. illustris* K. Schum. and *H. saldanhae* K. Schum., or usually three in *H. triflora*. They may be sessile or borne on stout peduncles and sometimes also short pedicels. Bracts are rare and resemble the stipules in shape and texture, but are much smaller. These bracts have been called "bracteoles" by some authors (e.g., Steyermark, 1972, 1974). The flowers are homostylous and apparently protrandrous. The duration of a single flower is unknown.

The calyx limb may be completely divided into four to six lobes, or as many as nine or ten in some species of subgenus *Illustres*; have a well-developed tube and short lobes, as in *Hillia costanensis*; or be completely absent in some individuals of some species, apparently never forming in the flower bud. This last condition may be what Schumann (1891) described as "caducous." The calyx limb typically persists until anthesis and often remains on the fruit. Size and shape of the calyx lobes frequently vary widely within a species.

The corollas may be salverform with relatively long slender tubes (subg. *Hillia*, subg. *Andinae*, subg. *Tetrandrae*), narrowly to broadly funnelform (subg. *Illustres*, subg. *Ravnia*), or tubular to inflated (subg. *Ravnia*). The salverform corollas have slender tubes and spreading lobes, and are white or sometimes flushed with pink or red in individuals of some species. They are strongly and sweetly fragrant at night, and are most likely pollinated by hawkmoths or other nocturnal vectors. The funnelform corollas have tightly reflexed lobes and are green sometimes flushed with yellow, pink, orange, dull purple, salmon, or bright red. Nothing is known about their odor or pollination, but they seem to be adapted for bat pollination. The tubular and inflated corollas also have tightly reflexed lobes and are red and odorless and apparently pollinated by birds. The corollas are membranaceous to thickly carnose; those of all species are glabrous throughout. There are usually four to six lobes, to as many as nine or ten in some species of subgenus *Illustres*. The number of lobes frequently varies within a species. Aestivation is contorted with the lobes oriented to the right, the less common condition in the Rubiaceae than leftward orientation (Robbrecht, 1988).

The stamens are inserted near the mouth of the corolla tube, or near the middle of the tube in subgenus *Tetrandrae*, subgenus *Andinae*, and some species of subgenus *Illustres*. They are usually equal in number to the corolla lobes, although they may be more or fewer in individuals of species of subgenus *Illustres*. The filaments are usually short, and the anthers are usually included. The anthers are bithecal and dehiscent by longitudinal slits, with the filaments attached near their bases. The pollen is reportedly 3-colporate (Robbrecht, 1988) or 3-porate (Andersson & Persson, 1991).

The style is straight and slender and is surrounded at the base by a low annular disk. The two stigmas are subcapitate or linear-elongate and usually positioned at or just above the anthers, or in subgenus *Tetrandrae* and subgenus *Andinae* in the lower part of the corolla tube below the anthers. The style is glabrous; the stigmas are usually papillose.

The inferior ovary is turbinate to cylindrical, with axile placentas that bear numerous ascendingly imbricated ovules. The ovary is sometimes narrowed to stipitate at the base.

FRUITS

The mature capsules are cylindrical, pale green to brown, woody, and smooth, or longitudinally ridged. Dehiscence is septicidal and basipetal, with the valves then opening longitudinally along the middle of the septum. The old valves often remain attached to the plant after the seeds are dispersed, with the fibrous exocarp and mesocarp separating from the papery endocarp. The capsules of most species terminate in a beak 1–10 mm long that is

composed of the enlarged and hardened disk and sometimes also an apical extension of the ovary above the attachment of the calyx limb. The capsules are stipitate in most species of subgenus *Illustres* and also in subgenus *Andinae* and *H. rivalis*. In some individuals the stipe is not evident on the flower, but elongates markedly during fruit development.

The narrowly rhombic seeds are strongly flattened with a small elliptic to rhombic embryo 1–3 mm long, and are partially edged by a thin membranaceous to papery margin or wing. A tuft of straight brown trichome-like processes or filaments about 1–3 cm long is attached to the acroscopic end. These processes have been regarded as outgrowths of the seed wall rather than "true" trichomes (Robbrecht, 1988). They apparently aid in wind dispersal, both by providing a sail and by attracting animals: hummingbirds pry open capsules of *Hillia parasitica* in Puerto Rico and remove seeds for nest construction, releasing numerous other seeds to the wind in the process (pers. obs.).

Cladistic Analysis

The classification presented here and for *Cosmibuena* (Taylor, 1992) is based on cladistic analyses of the individual species of *Hillia* and *Cosmibuena*, along with representatives of several genera of Cinchoneae. These analyses were directed at (1) the relationship among the epiphytic neotropical genera *Hillia*, *Cosmibuena*, and *Balmea* Martínez; (2) the relationship of *Hillia* to the Cinchoneae; (3) the relationships among the species of *Cosmibuena*; and (4) the relationships among the species of *Hillia*.

INGROUPS

The taxa analyzed were the four species of *Cosmibuena* recognized by Taylor (1992), *Balmea stormae* Martínez of northern Mesoamerica, and the twenty-four species of *Hillia* recognized in the present treatment.

OUTGROUPS

Four neotropical genera often classified in the Cinchoneae (Robbrecht, 1988; Andersson & Persson, 1991) were chosen as outgroups. These genera were chosen based on features shared with one or both genera of interest: *Ladenbergia* Klotzsch includes several species that are similar to *Cosmibuena* in stipule, inflorescence, floral, fruit, and seed morphology; *Ferdinandusa* Pohl species have inflorescence and corolla morphology similar to that of *Cosmibuena* and capsules similar to those of all three epiphytic genera; *Cinchona* L. has salverform corollas and capsules similar to those of all three epiphytic genera, though with acropetal dehiscence; and *Coutarea* Aubl. has funnelform white to pink corollas with five to six reflexed lobes and convolute or imbricate aestivation, and woody capsules with marginally winged seeds. The removal of *Coutarea* from the Cinchoneae to the Condamineeae has recently been proposed (Andersson & Persson, 1991); this genus is included in the present analysis based on the similarity of its corollas to some species of *Hillia*.

Two neotropical genera classified in other tribes, *Rondeletia* L. (Rondeletieae) and *Arcytophyllum* Roem. & Schult. (Hedyotideae), were chosen as outgroups based on their clear affinities outside of the Cinchoneae (Robbrecht, 1988), their capsular fruit, and their relatively recent morphological and systematic review. *Rondeletia* is here regarded in the wide sense as accepted by Lorence (1991); its morphology has also been summarized by Borhidi (1982), Kirkbride (1968), and Steyermark (1967). Characteristics of *Arcytophyllum* are based on the treatment by Mena (1990).

CHARACTERS

This analysis is based on morphological characters. The characters used and their states are shown in Table 1. Several of these (#1, 4, 5, 11, 26) are autapomorphies and were excluded in some analyses. The character states coded for each species are shown in Table 2.

Because examination of the relationships among the epiphytic groups was one of the goals of this analysis, habit was not included as a character. Quantitative characters were partitioned so that the number of polymorphic taxa was minimized. Polymorphic taxa were coded for the condition that was presumably less derived, based on outgroup comparison.

ANALYSIS

Several groups of analyses were made, using both PAUP (Swofford, 1990) and Hennig86 (Farris, 1988):

1. considering all species and using all of the characters listed in Tables 1 and 2, analyzed heuristically, with the characters treated variously as ordered or unordered;
2. considering all species and excluding the autapomorphic characters, analyzed heuristically, with the characters treated variously as ordered or unordered; and

TABLE 1. Characters and character states used in cladistic analyses. Characters denoted with an asterisk (*) are autapomorphic in individual species and were eliminated in some analyses; see text for further explanation.

1 dry color of plants*: 0 = green, 1 = reddish brown.
2 raphides: 0 = absent, 1 = present.
3 pubescence: 0 = plants with trichomes on vegetative portions, 1 = plants glabrous throughout.
4 bark texture*: 0 = smooth, 1 = wrinkled.
5 bark color*: 0 = brown, 1 = coppery red.
6 leaf size: 0 = more than 12 cm long, 1 = 6–12 cm long, 2 = 0.5–5 cm long.
7 leaf apex: 0 = acute to acuminate, 1 = rounded.
8 leaf texture: 0 = chartaceous, 1 = subcoriaceous, 2 = coriaceous.
9 leaf venation prominence: 0 = all prominent abaxially, 1 = primary and secondary veins prominent abaxially, 2 = primary vein prominent abaxially.
10 leaf venation pattern: 0 = pinnate, 1 = subpalmate.
11 number of secondary veins: 0 = 9–10 pairs, 1 = 3–8 pairs.
12 anisophylly*: 0 = absent, 1 = present.
13 stipule connation: 0 = interpetiolar, 1 = interpetiolar and intrapetiolar.
14 number of flowers: 0 = 3 to many, 1 = 1–3, 2 = 1.
15 corolla shape: 0 = salverform, 1 = funnelform, 2 = tubular, 3 = inflated.
16 corolla color: 0 = white, 1 = green, or green flushed with yellow or orange, 2 = green flushed with red, 3 = salmon red, 4 = bright red.
17 corolla aestivation: 0 = convolute, 1 = imbricate, 2 = valvate.
18 corolla lobe number: 0 = 4, 1 = 5–7, 2 = 8–10.
19 corolla lobe length: 0 = 8–15 mm, 1 = 16–25 mm, 2 = more than 25 mm.
20 corolla tube internal epidermis: 0 = glabrous, 1 = papillose.
21 calyx limb form: 0 = tube present, 1 = absent or divided to base.
22 anther position: 0 = included to slightly exserted, 1 = exserted.
23 stigma shape: 0 = subcapitate, 1 = with two linear branches, 2 = with two divergent, strongly flattened branches.
24 stigma position: 0 = below anthers, 1 = above anthers, included, 2 = above anthers, exserted.
25 stipe on capsule: 0 = absent, 1 = present.
26 capsule texture: 0 = papyraceous, 1 = woody.
27 capsule surface*: 0 = smooth to slightly longitudinally ridged, 1 = longitudinally winged.
28 capsule dehiscence: 0 = basipetal, 1 = acropetal.
29 comose seeds: 0 = absent, 1 = present.

3. considering subsets of species and excluding the autapomorphic characters, analyzed heuristically and with complete algorithms, with the characters treated variously as ordered or unordered.

TABLE 2. Character state coding used in the cladistic analyses. The characters and their states are numbered as defined in Table 1. "?" indicates missing data. Taxon abbreviations are as follows: ROND *Rondeletia* (Rondeletieae); ARCY *Arcytophyllum* (Hedyotideae); LADE *Ladenbergia* (Cinchoneae); FERD *Ferdinandusa* (Cinchoneae); COUT *Coutarea* (Cinchoneae or Condamineeae); CINC *Cinchona* (Cinchoneae); BALM *Balmea*; CGRA *Cosmibuena grandiflora*; CMAC *Cosmibuena macrocarpa*; CMAT *Cosmibuena matudae*; CVAL *Cosmibuena valerii*; HBON *Hillia bonoi*; HKIL *H. killipii*; HMAB *H. macbridei*; HMAM *H. macromeris*; HMAP *H. macrophylla*; HPAR *H. parasitica*; HWUR *H. wurdackii*; HPAN *H. panamensis*; HLOR *H. loranthoides*; HMAX *H. maxonii*; HPAL *H. palmana*; HTET *H. tetrandra*; HCOS *H. costanensis*; HFOL *H. foldatsii*; HGRA *H. grayumii*; HILL *H. illustris*; HPSA *H. psammophila*; HSAL *H. saldanhae*; HULE *H. ulei*; HALL *H. allenii*; HLON *H. longifilamentosa*; HPIT *H. triflora* var. *pittieri*; HOAX *H. oaxacana*; HRIV *H. rivalis*; HTRI *H. triflora* var. *triflora*.

	Characters					
	12345	67891	11111	11112	22222	2222
			0	12345	67890	12345	6789
ROND	00000	00000	00002	01000	00110	0000
ARCY	01000	20220	10002	02000	00110	0000
LADE	00000	00100	00000	02101	00210	1000
FERD	00000	00000	00000	00110	00010	1000
COUT	00000	10000	00001	00110	01010	1000
CINC	00000	00000	00000	02110	00210	0010
BALM	01100	10100	10002	40100	10110	1000
CGRA	01100	00120	10100	01111	00210	1000
CMAC	01100	00120	10100	01111	00210	1000
CMAT	01100	11220	10100	01111	00210	1000
CVAL	11100	11220	10120	00111	10210	1000
HBON	01100	00200	00020	00110	10010	??0?
HKIL	01111	10010	10020	00120	10010	1001
HMAB	01100	20220	10020	00110	10101	1001
HMAM	01100	00010	10020	00120	10010	??0?
HMAP	01100	00210	10020	00120	10010	1001
HPAR	01100	10120	10020	00120	10010	1001
HWUR	01100	10010	10020	00110	10010	??0?
HPAN	01100	21120	10020	00000	10100	1001
HLOR	01100	10220	10020	00010	10100	1001
HMAX	01100	11220	10020	00010	10100	1001
HPAL	01100	21220	10020	00000	10100	1001
HTET	01100	11120	10020	00010	10100	1101
HCOS	01100	10220	10021	10100	00021	1001
HFOL	01100	11220	10021	20100	10021	1001
HGRA	01100	00220	10021	10100	10010	1001
HILL	01100	00220	10011	10100	10021	1001
HPSA	01100	10220	10021	10100	10011	??0?
HSAL	01100	11120	10011	?0100	10011	??0?
HULE	01100	00221	10021	10200	10011	1001
HALL	01100	10220	10021	30100	10020	1001
HLON	01100	10220	10021	30110	11020	1001
HPIT	01100	10220	11013	40100	10020	1001
HOAX	01100	10221	10021	20100	10020	1?0?
HRIV	01100	10220	10021	20100	10021	1001
HTRI	01100	10220	10012	40100	10020	1001

Each subset of species included several outgroups, at least one member of each of the genera and subgenera under analysis, and all of the species of a particular focus group. *Cosmibuena* and each subgenus of *Hillia* were taken in turn as focus groups.

Autapomorphic characters were eliminated from the second and third sets of analyses because they were uninformative with regard to relationships among species. Subsets of species were used in the third group of analyses because the large number of species included in the full analyses, 36 in all, exceeds the size at which either cladistic analysis package is predicted to return a good response (Swofford, 1990). Only heuristic procedures could practically be employed with the full data set (first and second groups of analyses); one exhaustive search was attempted using Hennig86, but was unsuccessful and terminated after more than nine days of run time.

Results. Identical cladograms were obtained using both PAUP and Hennig86. Selected cladistic hypotheses will be presented and evaluated below; their systematic implications will be discussed in subsequent sections on classification and relationships. It should be clear from the hypotheses presented below that the morphological data available do not unequivocally indicate a single probable phylogenetic relationship among these species. However, these data do generally support the classification system proposed here; more detailed work is left to future systematists.

The first group of analyses found five equally most parsimonious cladograms. One of these is shown in Figure 1. In all of these cladograms, *Balmea* was grouped with *Hillia* subg. *Ravnia*; *Hillia–Balmea* was monophyletic; *Cosmibuena* was arranged as a grade immediately basal to *Hillia*; *Hillia–Balmea–Cosmibuena* was monophyletic; and *Hillia* subg. *Tetrandrae* was monophyletic. The strict consensus of these five cladograms is shown in Figure 2. These five cladograms differed in the arrangement of the species of subgenus *Hillia*, which were variously arranged as a clade or grade; in the relationships among the species of subgenus *Illustres*, which were arranged as a grade in all cladograms; and in the relationships of species of subgenus *Illustres* with those of subgenus *Ravnia*.

The second group of analyses found three equally most parsimonious cladograms. One of these is shown in Figure 3. The strict consensus cladogram obtained from these analyses is shown in Figure 4. In all of these cladograms, *Cosmibuena* was arranged as a monophyletic group placed within *Hillia*; *Hillia–Cosmibuena* was monophyletic; *Balmea* was placed immediately basal to this group; *Hillia–Cosmibuena–Balmea* was monophyletic; and subgenus *Tetrandrae* was monophyletic. The cladograms differed in the arrangement of species of subgenus *Hillia*, which were always arranged as a grade; in the arrangement of the species of subgenus *Illustres*, which were always arranged as a grade; and in the relationships of the species of subgenus *Illustres* with those of subgenus *Ravnia*.

Results from the third group of analyses are not presented here. These did not contradict previous analyses and added no information.

Tribal Classification of *Hillia*

The position of *Hillia* within the Rubiaceae has been the subject of significant disagreement, and its placement has been altered as ideas about the systematics of the family have evolved.

Schumann (1891) agreed with earlier authors in placing *Hillia* in the Cinchoneae DC., distinguished by capsular fruit with ascendingly imbricated winged seeds, of the subfamily Cinchonoideae Raf., distinguished by numerous ovules in each locule.

Verdcourt (1958) proposed the next, extensively revised classification of the Rubiaceae, utilizing new characters and assumptions. Verdcourt placed *Hillia* in his subfamily Rubioideae, which was distinguished by the presence of raphides. *Hillia* occupied an isolated position within this subfamily and was not classified further, although Verdcourt suggested that it might be placed in its own monotypic tribe.

Bremekamp (1966) reviewed the Rubiaceae in further detail, drawing on his own and Verdcourt's work and basing his classification on various characteristics including sculpturing of the testa walls and the presence or absence of raphides, which he considered to have evolved only once in the family. Bremekamp placed *Hillia* in subfamily Hillioideae Bremek. ex S. P. Darwin along with *Ravnia* Oerst. and *Deppea* Schltdl. & Cham., based on the presence in all three genera of raphides, contorted corolla aestivation, and a distinctive exotestal cell structure that was otherwise found only in *Gleasonia* Standl. *Deppea* has since been shown to have little relationship to *Hillia* and has been placed in its own tribe (Kirkbride, 1982) or more recently in the Hamelieae DC. (Bremer, 1987). *Ravnia* has been synonymized with *Hillia* (Taylor, 1989), and thus *Hillia* occupies an isolated position in Bremekamp's classification.

FIGURE 1. One of five most parsimonious putative phylogenies of *Hillia* and *Cosmibuena* species obtained from the first set of analyses as described in the text, based on the full character set presented in Table 2. Analysis was heuristic (Hennig86: mhennig* and branch-breaking options); characters were treated as ordered; polarity was determined by majority rule among outgroups. Numbers designating characters and their states are defined in Table 1; four-letter codes designating taxa are defined in Table 2. Black rectangles indicate synapomorphies that are not reversed on the cladogram; open rectangles indicate synapomorphies with reversals on the cladogram; crosses indicate reversals; parallel lines indicate parallelisms. See also discussion in the text and Figure 2.

The most recent comprehensive classification of the Rubiaceae was proposed by Robbrecht (1988). Raphides probably have arisen repeatedly in the Rubiaceae (Robbrecht, 1988), and he again placed *Hillia* in the Cinchonoideae. Robbrecht indicated that within this subfamily *Hillia* is related to the Cinchoneae but "reduced," in fact "an extreme case of this trend." He maintained *Hillia* in its own tribe, citing "many characters justifying its separation as a monogeneric tribe," but without

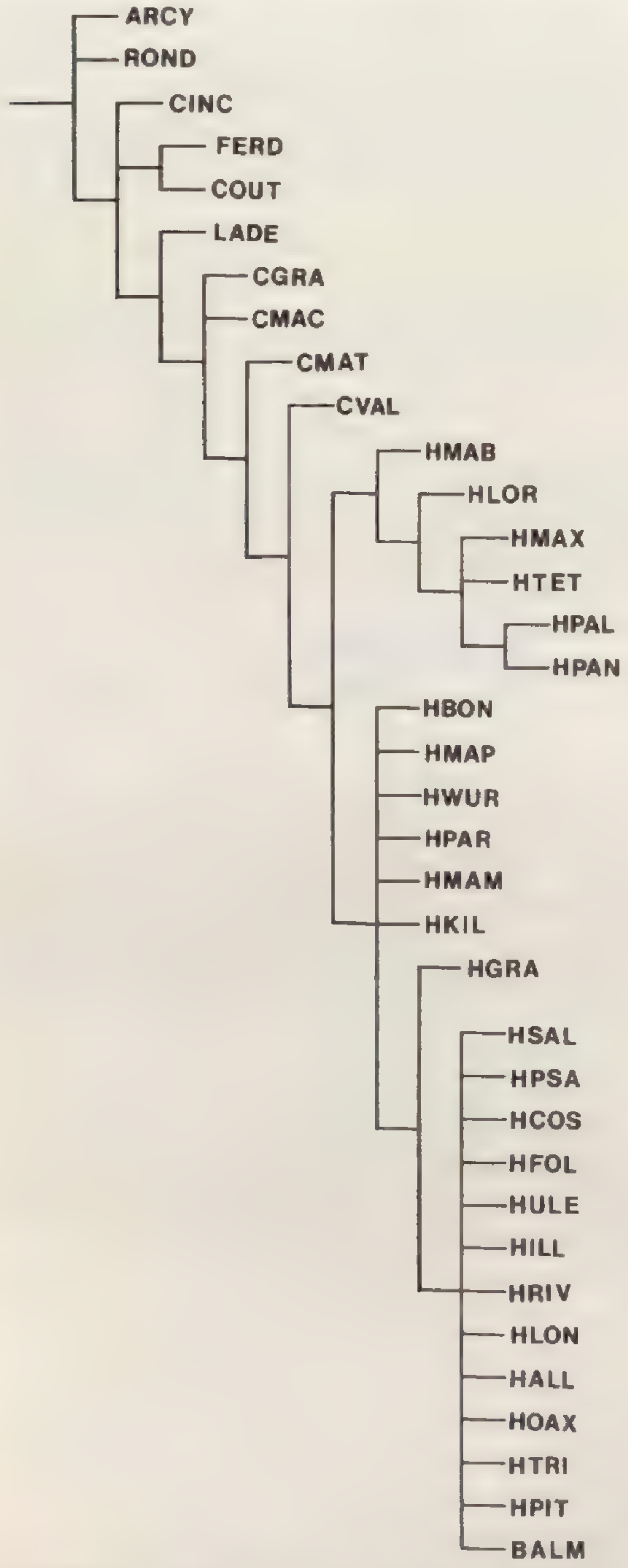

FIGURE 2. Strict consensus tree of the five cladograms obtained in the first set of analyses described in the text. Four-letter codes designating taxa are defined in Table 2.

listing them. This classification apparently depends heavily on the comose seeds. Robbrecht concluded that these structures are better regarded as outgrowths or extensions of the testa wall, and thus homologous to the testa walls of other species rather than trichomes. However, he did not otherwise explain the difference between these epidermal outgrowths and other epidermal outgrowths classified as trichomes.

The position of *Hillia* within the Rubiaceae has been examined in detail by Andersson & Persson (1991) in a cladistic analysis of genera that have been proposed by various authors for inclusion in the Cinchoneae. Their character set is extensive and reliable, although the results of their analyses do not seem unequivocal. Andersson & Persson found *Hillia* to be variously grouped as a member of their Cinchoneae s. str., as a sister group of this tribe, or as a more distant taxon. They concluded that *Hillia* is closely related to the Cinchoneae, with which it shares fruit type and similar sculpturing of the radial exotestal wall, but maintained *Hillia* in its own tribe, which they considered possibly the sister group of the Cinchoneae.

Hillia is separated from the Cinchoneae s. str. in this scheme by the sculpturing pattern of the inner tangential testa wall; solitary rather than several flowers; and seeds with scanty endosperm and comose appendages. Of these, only the comose seed appendages are unique in the entire data set and the Rubiaceae. Several other characteristics are shared with some members of the Cinchoneae s. str., where they are considered derived: wood rays 4-seriate; pollen porate or colporate; corolla aestivation contorted; pollen tectum imperforate; and habit epiphytic. Several characteristics used by Andersson & Persson to distinguish *Hillia* are here considered inaccurate, although this information may not have been available to them: calyx lobes divided to the base are also found in *Cosmibuena* and *Balmea*, while many species of *Hillia* completely lack a calyx limb and one species has a well-developed calyx tube; and fusiform seeds may not be confined to *Hillia* if the variation in seed shape and margin among all species of Cinchoneae, notably *Cosmibuena*, is considered.

Thus *Hillia* seems closely related to genera presently classified in the Cinchoneae s. str. and may be derived from within this group. *Hillia* seems to represent a line characterized by adaptations to an epiphytic habit, many of which are unusual or uniquely derived. Most of these features are not found in the Cinchoneae and therefore are used to exclude *Hillia* from that group, but the characters on which this decision is based do not seem conclusive. Homoplasious characters, as the exotestal wall sculpturing and raphides appear to be (cf. Bremekamp, 1966), are poor indicators of relationship, while autapomorphic features such as the comose seeds do not indicate any relationship.

Classification of *Hillia* therefore seems to depend on character weighting: this genus can be isolated in a monotypic tribe based on its uniquely derived features, or it can be included as a relatively derived member of the Cinchoneae, based on the

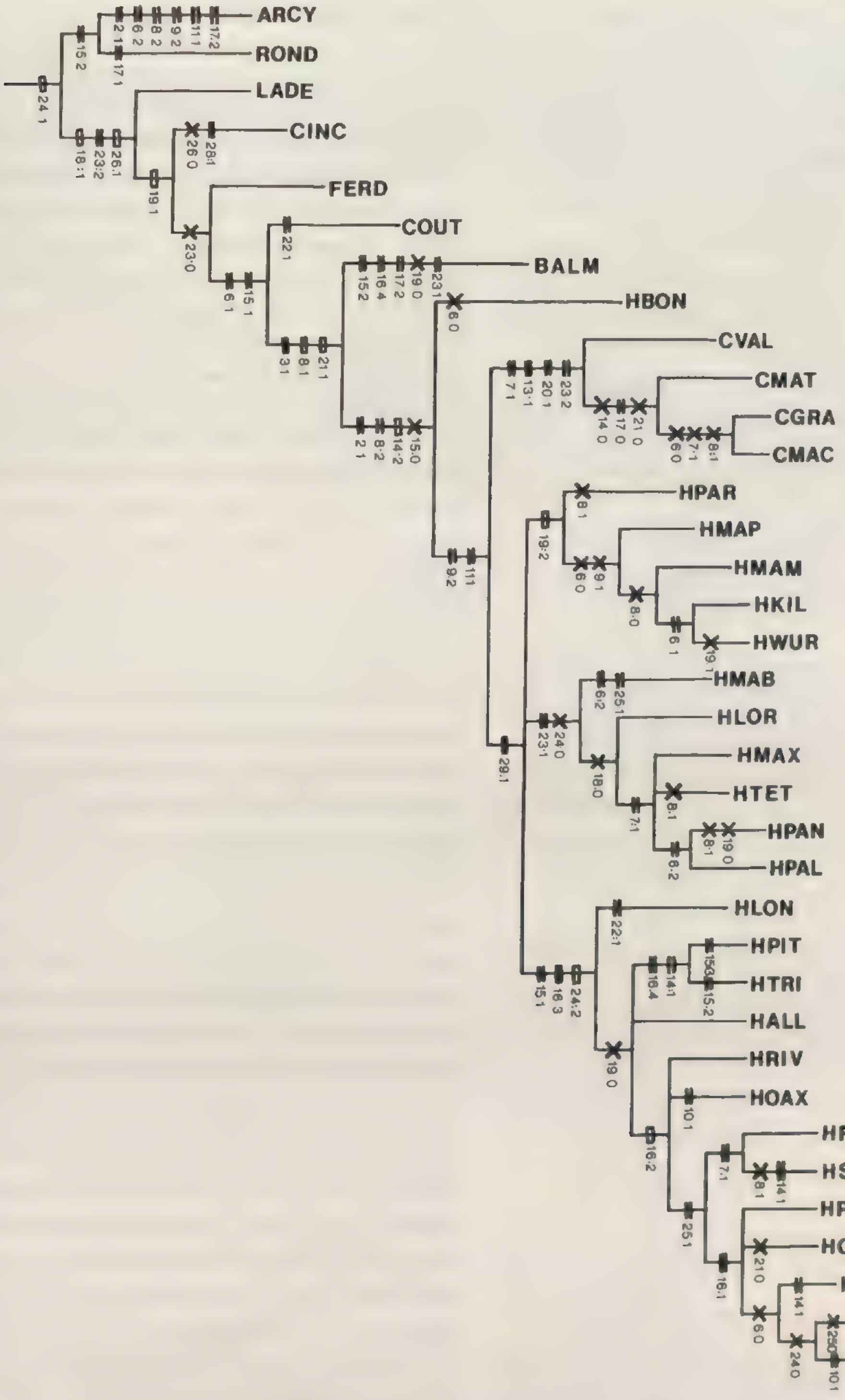

FIGURE 3. One of three most parsimonious putative phylogenies of *Hillia* and *Cosmibuena* species obtained from the second set of analyses as described in the text, based on a subset of the characters presented in Table 2, excluding autapomorphic characters. Analysis was heuristic (Hennig86: mhennig* and branch-breaking options); characters were treated as unordered; polarity was determined by regarding *Ladenbergia* as ancestral. Numbers designating characters and their states are defined in Table 1; four-letter codes designating taxa are defined in Table 2. Symbols are the same as in Figure 1. See also Figure 4 and discussion in the text.

characteristics it shares with that group. Isolating *Hillia* in a monotypic tribe requires the assumption that the characteristics that distinguish it are all derived independently from the character states seen in the Cinchoneae, rather than as part of a transformation series. However, the comose seeds of *Hillia* and the narrowly shaped, strongly erose seed margins of *Cosmibuena*, terminating in sparse filaments that resemble the numerous filaments of *Hillia*, need not have arisen independently, but may be steps in a transformation series. If the characters are viewed in this way, isolating *Hillia*

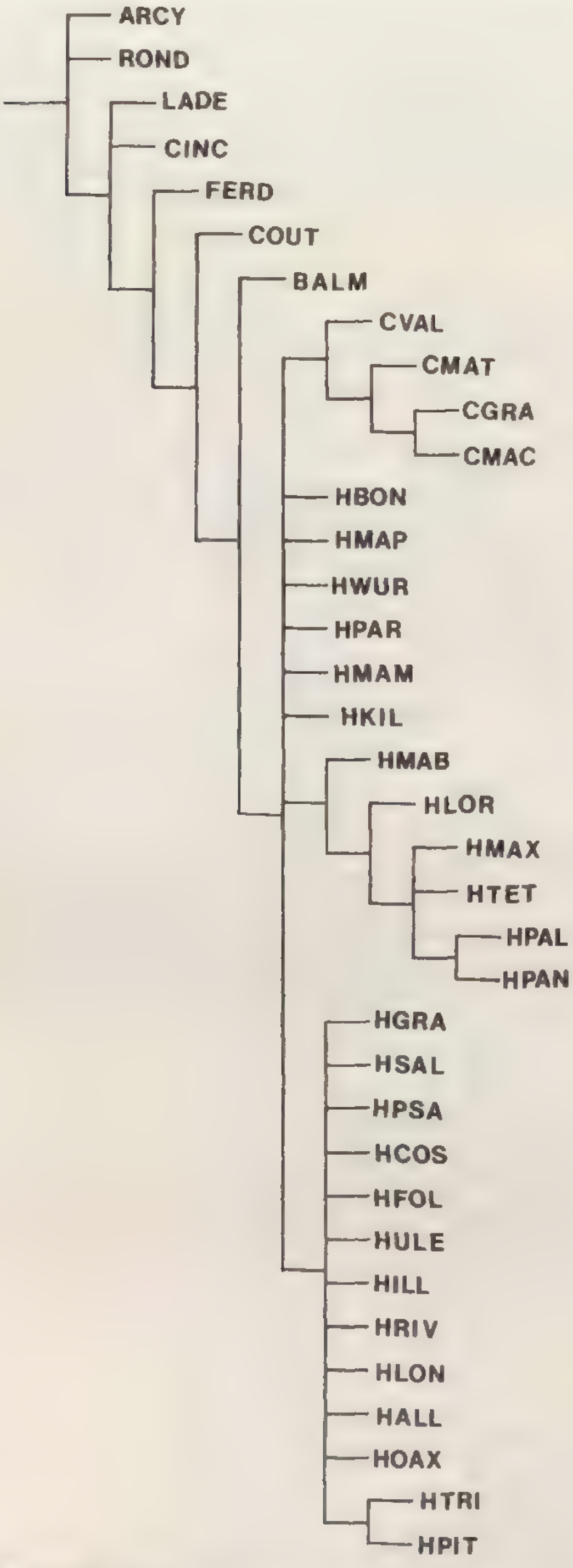

FIGURE 4. Strict consensus tree of the three cladograms obtained in the second set of analyses described in the text. Four-letter codes designating taxa are defined in Table 2.

results in an arbitrary separation of the derived end of an evolutionary trend toward reduction, in order to emphasize its distinctness rather than its relationships. Classification seems more useful when it reflects relationships rather than emphasizes distinctness, and *Hillia* is here considered a member of the Cinchoneae, probably closely allied with *Balmea* and *Cosmibuena*.

GENERIC RELATIONSHIPS OF *HILLIA*

As discussed in the previous section, the relationships of *Hillia* are with the Cinchoneae (Robbrecht, 1988; Andersson & Persson, 1991). Most of the characteristics that distinguish *Hillia* are either unique or found in many other rubiaceous genera and are therefore not good indicators of relationship. However one, epiphytic habit, is unusual within the Rubiaceae yet found in a few other genera (Robbrecht, 1988), and thus is potentially informative. Other epiphytic genera sometimes placed in the Cinchoneae are *Balmea*, *Cosmibuena*, and *Hymenodictyon* Wall.

Hymenodictyon includes about 20 occasionally epiphytic species found in Asia, Indonesia, Madagascar, and Africa. These differ markedly from *Hillia* in their small triangular stipules; numerous flowers borne in a dense, bracteate, spicate or capitate inflorescence; reduced funnelform to campanulate corollas with valvate aestivation; fusiform to elliptic stigmas that function as a pollen presentation mechanism; loculicidal capsules; lack of raphides; and vestiture of well-developed trichomes (Verdcourt, 1988). Based on these characters, *Hymenodictyon* does not seem closely related to *Hillia*.

Balmea is a monotypic genus found in southern Mexico and adjacent Guatemala that shares with species of *Hillia* a glabrous, rather succulent, sometimes epiphytic habit; the presence of raphides (Andersson, pers. comm.); a calyx limb almost completely divided into five lobes; a tubular to funnelform dark red corolla with five convolute lobes that are strongly reflexed; shortly linear styles; and beaked, cylindrical, septicidally dehiscent capsules. *Balmea* differs from *Hillia* in its small triangular stipules; eight or more flowers borne in pedunculate branched cymes; capsule valves that are partially divided at the apex; and seeds that are not comose (Standley & Williams, 1975). *Balmea* may be closely related to *Hillia* (cf. Figs. 1–4).

Cosmibuena is a genus of four species found from southern Mexico to Peru that share with *Hillia* a glabrous, succulent, usually epiphytic habit; the presence of raphides; large ligulate to oblanceolate stipules; three to several flowers borne in a terminal cyme or fascicle; salverform white corollas; porate pollen (Andersson & Persson, 1991); and beaked, cylindrical, septicidal capsules. *Cosmibuena* differs from *Hillia* in its intrapetiolarly fused stipules; usually shortly tubular calyx limb (completely divided in *C. valerii* (Standl.) C. M. Taylor); quincuncial corolla aestivation; bilobed

densely papillose stigmas; sculpturing of the inner tangential testa wall; and seeds that are not comose (Taylor, 1992). *Cosmibuena* seems closely related to *Hillia* and also to *Balmea*. Cladistic analysis indicates several possible relationships among these three epiphytic genera, from polyphyly (Andersson & Persson, 1991) to forming a monophyletic group (Figs. 1–4). The presence of raphides in *Cosmibuena* has been overlooked by some authors (e.g., Bremekamp, 1966; Robbrecht, 1988): the segregation of these genera has been based in part on this one feature and deserves reexamination. However, *Cosmibuena* also shares some features with *Ladenbergia* and other genera of Cinchoneae that are not found in *Hillia*, so the systematics of this group are far from resolved.

Infrageneric Systematics

Five subgenera are recognized here, three newly described. The delimitation of these subgenera is based primarily on the shape, number of lobes, and color of the corolla. The corolla features are generally correlated with similarities in stigma form and position relative to the anthers and the top of the corolla tube. The stigma and corolla characters may be shared in unrelated species with similar pollination syndromes, but stigma condition in conjunction with corolla form appears to be useful for phylogenetic inference in the Rubiaceae (Bremer & Jansen, 1990). The geographic coherence of the resulting subgenera and the presence of additional features shared by members of each group support the classification proposed here.

Subgenus *Tetrandrae* is the most clearly delimited of these groups. It is distinguished by its white salverform corollas with four lobes. These flowers are fragrant at night and are presumably pollinated by sphingids or other types of moths. White salverform corollas probably represent the ancestral condition in the genus and are also found in subgenus *Hillia* and subgenus *Andinae*. The four-lobed condition is otherwise unknown in *Hillia* and apparently represents a reduction from the five- to ten-lobed corollas that characterize the other subgenera. The species of subgenus *Tetrandrae* additionally share relatively short styles and linear stigmas positioned below the middle of the corolla tube and far below the anthers, which are situated at the mouth of the tube. This stigma morphology and position are otherwise found only in *H. macbridei* Standl. of subgenus *Andinae*, which differs in its five-lobed corolla. Within subgenus *Tetrandrae* most species have rounded leaf apices and corolla lobes. Several species of this subgenus also have relatively small leaves and flowers, although they are not the only such reduced taxa.

Subgenus *Hillia* appears to be the basalmost group in the genus. This subgenus is characterized by salverform white corollas with five to six lobes. The flowers are strongly fragrant at night and are presumably pollinated by sphingids or other moths. The bilobed stigmas are subcapitate to somewhat elongated and positioned above the anthers. Several species have leaf domatia and well-marked secondary leaf veins, and the higher-order venation is also well marked in *H. bonoi* Steyerm. A wide range of leaf and flower sizes is represented within this subgenus, including the largest flowers in the genus (*H. macromeris* Standl.). Subgenus *Hillia* may be a diverse basal assemblage of species rather than a monophyletic group; the characters available are insufficient to distinguish between these possibilities.

Hillia macbridei appears to be intermediate between subgenus *Hillia* and subgenus *Tetrandrae* in its floral morphology: it shares the characteristic stigma position and morphology of subgenus *Tetrandrae*, while its corollas with five to six long narrow lobes are characteristic of subgenus *Hillia*. Vegetatively this species is unique in its reduced lanceolate leaves that are acute and usually stiffly coriaceous. All cladistic analyses consistently grouped this species as the sister group of subgenus *Tetrandrae*. This species is here placed in its own subgenus, subgenus *Andinae*.

Subgenus *Illustres* and subgenus *Ravnia* share funnelform corollas with five to ten lobes and subcapitate stigmas positioned at or just above the anthers. This stigma morphology is also shared with some species of subgenus *Hillia*. These two subgenera appear to be more closely related to each other than to the other subgenera of *Hillia*, and relatively more derived.

Subgenus *Illustres* is characterized by corollas that are predominantly green, although they may be flushed with yellow, orange, pink, or red. Nothing is known of the floral biology of these species, but the flowers appear to be adapted for pollination by bats. With the exception of *H. grayumii* C. M. Taylor, the species of this section are also characterized by stipitate fruit. Subgenus *Illustres* includes the widest variation in leaf form, anther position, and number of corolla lobes, although there appear to be no patterns or trends in this variation. Subgenus *Illustres* (excluding subg. *Ravnia*) may represent a grade rather than a monophyletic group; the morphological characters avail-

able are insufficient to distinguish between these possibilities.

Subgenus *Ravnia* is characterized by red corollas with six to seven lobes. The odorless flowers are presumably pollinated by birds and thus diurnal. This group was discussed in detail by Taylor (1989). Two species have been added subsequently to that treatment (Taylor, 1991), expanding the geographic range of the subgenus but not altering its characteristics. This subgenus is apparently the most derived.

The separation of subgenus *Ravnia* from subgenus *Illustres* is based exclusively on flower color and presumed pollination syndrome. Given the similarity between the two floral morphologies, red diurnally pollinated flowers could have arisen more than once. Subgenus *Ravnia* is here assumed to represent a monophyletic group, but further study may show that some of its species are better classified in subgenus *Illustres*.

Taxonomic Treatment

This study is based on study of herbarium specimens from the institutions listed in the acknowledgments, supplemented by fieldwork in Puerto Rico, Hispaniola, Dominica, Costa Rica, and Colombia. Measurements of soft parts given here are based on dried specimens; plants of *Hillia* are fleshy, and shrinkage of about 8–10% in soft parts accompanies the preparation of herbarium specimens.

Hillia Jacquin, Enum. Syst. Pl. 3. 1760. TYPE: *Hillia parasitica* Jacq.

Fereiria Vell. ex Vand., Fl. Lusit. Bras. Spec. 21, t. 1, fig. 8. 1788. TYPE: *Fereiria vellozoana* Schult. & Schult. f., Syst. Veg. 7: 83. 1829. [= *Hillia parasitica* Jacq.]

Saldanha Vell., Fl. Flum. 141. 1825. TYPE: *Saldanha nobilis* Vell. [= *Hillia parasitica* Jacq.], lectotype designated here.

Ravnia Oerst., Vidensk. Meddel. Dansk Naturhist. Foren. Kjoebenhavn 1852: 49. 1853. TYPE: *Ravnia triflora* Oerst. [= *Hillia triflora* (Oerst.) C. M. Taylor.]

Shrubs, small trees, suffrutescent herbs, or lianas, slightly to strongly succulent, epiphytic or sometimes terrestrial or rarely rheophytic (*H. rivalis*), erect or sometimes clambering, glabrous throughout, with raphides; stems quadrate, usually becoming terete; bark smooth or rarely papyraceous and wrinkled circumferentially to peeling (*H. killipii*), gray to brown or sometimes red-brown or rarely coppery red (*H. killipii*). Leaves opposite, decussate, isophyllous or rarely anisophyllous (*H. triflora* var. *pittieri*), petiolate or rarely subsessile (*H. costanensis*); blades elliptic to very narrowly elliptic or ovate, entire, fleshy, drying membranaceous to coriaceous, rarely with pocket or crypt domatia (*H. bonoi*, *H. macrophylla*); secondary veins pinnate or rarely subpalmate (*H. oaxacana*, *H. ulei*), ascending, distal veins usually looping to interconnect, margins flat or rarely revolute (*H. bonoi*, *H. macbridei*, *H. rivalis*); stipules interpetiolar, caducous or those subtending flowers sometimes persisting until anthesis, ligulate to oblanceolate, membranaceous to subcoriaceous, with fine subparallel subpalmate venation, becoming pale green to white or sometimes reddened just before falling. Flowers terminal, solitary or rarely 2–3 in a subsessile cyme (*H. illustris*, *H. saldanhae*, *H. triflora*), homostylous, apparently protandrous, with peduncles and pedicels stout, sometimes subtended by bracts, these similar to stipules but reduced in size; calyx with limb deeply divided or sometimes lacking or rarely with a well-developed tube and short lobes (*H. costanensis*), green, with lobes 4–10, sometimes variable in number within a species or an individual plant; corollas salverform (subg. *Hillia*, subg. *Andinae*, subg. *Tetrandrae*) to funnelform (subg. *Illustres*, subg. *Ravnia*), tubular (subg. *Illustres*, subg. *Ravnia*), or swollen (*H. triflora*), white (subg. *Hillia*, subg. *Andinae*, subg. *Tetrandrae*) to green sometimes flushed with yellow, pink, orange, or dull purple (subg. *Illustres*), or salmon to bright red (subg. *Ravnia*), with lobes 4 (subg. *Tetrandrae*) to 10, when more than 6 then sometimes variable in number within a species or individual plant, aestivation contorted to right; stamens usually equal in number to corolla lobes, inserted near top or middle of corolla tube, the filaments flattened to winged, very short to lacking or elongated, the anthers narrowly oblong to ellipsoid, bithecal, dehiscent by longitudinal slits, attached near base, partially to fully included or rarely exserted (*H. longifilamentosa*); ovary inferior, bilocular, turbinate to cylindrical, sometimes stipitate, the ovules numerous, vertically imbricate, borne on axile placentas; disk annular; styles straight; stigmas 2, subcapitate to shortly or elongated-linear, papillose, positioned at or just above or sometimes well below anthers. Fruit capsular, cylindrical, woody, smooth or sometimes longitudinally ridged to rarely winged (*H. tetrandra*), usually with beak formed by old disk and sometimes also the elongated ovary apex, septicidally and basipetally dehiscent; seeds flattened, elliptic to rhombic, with membranaceous to papyraceous

marginal wings, with tufted multiseriate filaments ("trichomes") extending from cell wall at acropetal end.

Twenty-four species, southern Mexico and Antilles to Peru, Bolivia, and southeastern Brazil, in moist to wet forest zones at 0–2400 m.

In his generic description of *Saldanha*, Vellozo described the calyx as five-parted with subulate lobes, the corolla as five-lobed, and the stamens as six. He named two species, *S. illustris* Vell. and *S. nobilis*. The identities of both species are clear (Steyermark, 1972). Both of them typically have six calyx and corolla lobes and six stamens; the generic description thus applies equally well (or poorly) to each of them. Although Vellozo's generic description is somewhat weighted toward *S. illustris*, his description and illustration of a plant with five calyx and corolla lobes are either inaccurate, or depict an atypical individual. His illustration and description of *S. nobilis* accurately depict *H. parasitica*, and that species is therefore chosen as the lectotype.

Key to the Subgenera of *Hillia*

1a. Corollas salverform, white or pale green, sometimes pink on surfaces exposed in bud.
  2a. Corolla lobes 5–6; stigmas subcapitate to linear, 0.5–4 mm long, positioned above or below anthers.
    3a. Stamens inserted near top of corolla tube; stigmas subcapitate to shortly linear, 0.5–2 mm long, positioned just above anthers ..... 1. subgenus *Hillia*
    3b. Stamens inserted near middle of corolla tube; stigmas linear, 2–4 mm long, positioned below anthers ..... 2. subgenus *Andinae*
  2b. Corolla lobes 4; stigmas linear, 2–6 mm long, positioned below anthers ..... 3. subgenus *Tetrandrae*

1b. Corollas funnelform to tubular or inflated, green, green flushed with yellow, pink, orange, or dull purple, or salmon to bright red.
  4a. Corollas funnelform, green or green flushed with yellow, pink, orange, or dull purple ..... 4. subgenus *Illustres*
  4b. Corollas funnelform to tubular or inflated, salmon to bright red ... 5. subgenus *Ravnia*

Key to the Species of *Hillia*

1a. Leaf blades narrowly elliptic to lanceolate, 3–4 times as long as wide, 0.6–3 cm long.
  2a. Leaf blades lanceolate, thickly coriaceous; plants of Peru and Ecuador ..... 7. *H. macbridei*
  2b. Leaf blades elliptic to narrowly elliptic, subcoriaceous to coriaceous; plants of Mexico to western Panama ..... 12. *H. panamensis*

1b. Leaf blades elliptic to suborbicular or obovate, less than 3 times as long as wide, 2–22 cm long.
  3a. Primary, secondary, and sometimes tertiary venation prominulous to prominent on abaxial leaf surface.
    4a. Primary, secondary, and tertiary venation prominent ..... 4. *H. bonoi*
    4b. Primary and secondary but not tertiary venation prominent or prominulous.
      5a. Bark coppery red, peeling and wrinkled in small circumferential rings, especially on young twigs ..... 5. *H. killipii*
      5b. Bark gray-brown or dull red-brown, not peeling or wrinkled in circumferential rings.
        6a. Leaf blades 4.5–10 cm long, 1.8–5 cm wide; corolla lobes 12–26 mm long ..... 1. *H. wurdackii*
        6b. Leaf blades 9–22 cm long, 3–10 cm wide; corolla lobes 35–90 mm long.
          7a. Corolla lobes 35–54 mm long ..... 2. *H. macrophylla*
          7b. Corolla lobes 75 90 mm long ..... 3. *H. macromeris*
  3b. Leaf venation plane or sometimes the midrib prominulous on abaxial leaf surface.
    8a. Leaf blades rounded to obtuse at apex.
      9a. Corollas salverform, lobes 4; stigmas 5–15 mm long, held below anthers.
        10a. Leaf blades subcoriaceous to coriaceous; capsules with well-developed ridges or wings to 1 mm high; Greater Antilles and southern Mexico to northern Nicaragua ..... 9. *H. tetrandra*
        10b. Leaf blades coriaceous, often thickly so; capsules smooth or with slight longitudinal ridging; southern Nicaragua to northeastern South America.
          11a. Corolla tubes 42–55 mm long; lobes 15–27 mm long ..... 10. *H. maxonii*
          11b. Corolla tubes 35–40 mm long; lobes 8–12 mm long ..... 11. *H. palmana*
      9b. Corollas funnelform, lobes 5–9; stigmas 1–2 mm long, held above anthers or exserted.
        12a. Leaf blades subcoriaceous; stigmas included, held 2–3 mm below top of corolla tube ..... 17. *H. saldanhae*
        12b. Leaf blades thickly coriaceous; style exserted 4–5 mm beyond top of corolla tube ..... 18. *H. foldatsii*
    8b. Leaf blades acute to acuminate at apex.
      13a. Leaf venation subpalmate, with all secondary veins arising below middle of blade.
        14a. Corolla tubes red, ca. 38 mm long, the lobes 2.5 mm long; plants of southern Mexico ..... 20. *H. oaxacana*

14b. Corolla tubes green to yellow-green, 28–39 mm long, lobes 6–7 mm long; plants of Amazonian South America ..... 16. *H. ulei*

13b. Leaf venation pinnate, with at least one pair of secondary veins arising distal to middle of blade.

15a. Leaves strongly anisophyllous, the larger leaf at a node at least 1.5 times as long as the shorter leaf ..... 24b. *H. triflora* var. *pittieri*

15b. Leaves isophyllous or slightly anisophyllous, the larger leaf at a node less than 1.4 times as long as the shorter leaf.

16a. Calyx limb 36–68 mm long, with tube 33–56 mm long; leaf blades rounded to slightly cordate at base ..... 19. *H. costanensis*

16b. Calyx limb 3–36 mm long and lobed to base, minute and truncate to dentate, or lacking; leaf blades rounded to attenuate at base.

17a. Flowers (1–)3; corollas tubular to slightly inflated, red ..... 24a. *H. triflora* var. *triflora*

17b. Flowers solitary(–3); corollas salverform or funnelform, white or green or orange-red.

18a. Calyx lobes narrowly triangular to linear, 18–36 mm long ..... 23. *H. rivalis*

18b. Calyx lobes lacking or triangular to oblanceolate, orbicular, or ligulate, 3–35 mm long.

19a. Corollas salverform, white or pale green, sometimes pink on surfaces exposed in bud.

20a. Corolla lobes (5–)6(–9), the tubes (38–)60–125 mm long; plants of the Antilles and South America ..... 6. *H. parasitica*

20b. Corolla lobes 4, the tubes 45–75 mm long; plants of southern Mexico and Central America ..... 8. *H. loranthoides*

19b. Corollas funnelform, green to red-orange.

21a. Corollas red to orange; plants of Costa Rica and Panama.

22a. Corolla lobes 13–17 mm long; free portion of filaments 9–10 mm long ... 22. *H. longifilamentosa*

22b. Corolla lobes 6–10 mm long; free portion of filaments ca. 1 mm long ..... 21. *H. allenii*

21b. Corollas green to yellow-green; plants of Costa Rica to South America.

23a. Leaf blades 4.5–6.5 cm long ..... 14. *H. psammophila*

23b. Leaf blades 8.5–15 cm long.

24a. Calyx limb 9–35 mm long, lobed to base ..... 15. *H. illustris*

24b. Calyx limb lacking or to 0.5 mm long, truncate to dentate ..... 13. *H. grayumii*

1. **Hillia** subg. **Hillia.**

Calyx limb lacking or with 5–6 lobes; *corollas* salverform, white or pale green on surfaces exposed in bud, sometimes flushed with pink or red, becoming yellowed with age, the lobes 5–6; *stamens* attached near apex of corolla tube; anthers subsessile; *stigmas* subcapitate to shortly linear, positioned just above anthers.

Seven species in the Antilles and South America.

1. Hillia wurdackii Steyermark, Mem. New York Bot. Gard. 23: 294. 1972. TYPE: Peru. Amazonas: Bongara, on road to La Rioja 5 km N of N end of Lake Pomacocha, 2000 m, 8 Oct. 1964, *P. C. Hutchinson & J. K. Wright 6799* (holotype, VEN not seen; isotypes, F, K not seen, MO, NY, UC not seen, US, USM not seen).

Shrubs or small trees to 7 m tall; bark gray-brown to red-brown, smooth. Leaf blades elliptic to somewhat ovate, 4.5–10 cm long, 1.8–5 cm wide, acuminate at apex with tip 5–10 mm long, cuneate to broadly obtuse at base, chartaceous; secondary veins pinnate, 4–8 pairs, midrib and secondary veins somewhat impressed adaxially, prominent abaxially, without domatia; margins flat; petioles 6–11 mm long; stipules 14–40 mm long, 6–18 mm wide, sometimes becoming red. Flowers solitary; peduncles 1–1.5 mm long; bracts lacking or ca. 3 × 1 mm; calyx limb lacking; corollas white or pale green on surfaces exposed in bud, the tubes 40–58 mm long, the lobes 5–6, (12)20–26 mm

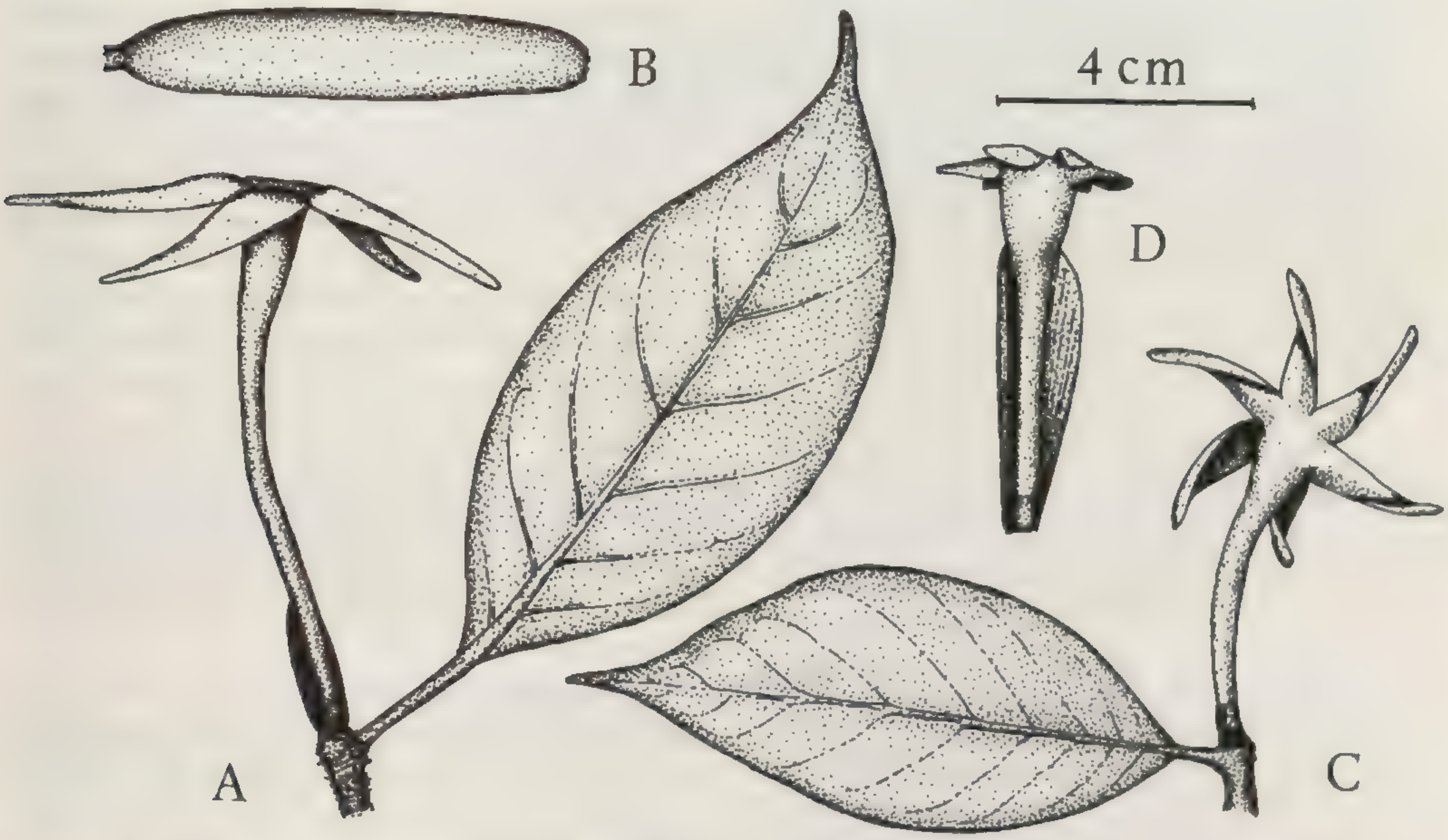

FIGURE 5. A, B. *Hillia killipii* Standl.—A. Habit with flower.—B. Capsule. C, D. *Hillia wurdackii* Steyerm.—C. Habit with flower.—D. Flower with stipule (floral). A, from *Killip & Smith 26085* (NY); B, from *Camp E-2405* (US); C, from *Hutchison et al. 6799* (MO); D, from *Woytkowski 8236* (MO). All to same scale.

long, 9–12 mm wide, elliptic to triangular, acute; anthers 5–6, subsessile, 10–11 mm long, with tips positioned 3–5 mm below top of corolla tube; ovary 5–10 mm long; stigmas subcapitate, 2–3 mm long, positioned immediately above anthers. Capsules 6.5–8 cm long including beak 6–7 mm long, 1–1.3 cm diam., not stipitate, smooth; seeds ca. 2 × 0.8 mm, with filaments 12–13 mm long. Figure 5C, D.

Habitat, phenology, and distribution (Fig. 3). Ecuador and Peru, in wet forests at 2000–2400 m. Collected in flower in June and October.

Hillia wurdackii is similar to *H. macrophylla*, *H. macromeris*, and *H. killipii* in its chartaceous to coriaceous leaves with the secondary veins prominent on the abaxial surface, but differs from the first two species in its smaller flowers and from the last in its smooth bark. This species may be only a small-flowered variant of *H. macrophylla*.

One collection, *Woytkowski 8236* (Fig. 5D), is classified here provisionally but differs from other collections of *Hillia wurdackii* in its relatively short corolla lobes, only 12 mm long.

Additional specimens examined. ECUADOR. **Pastaza:** trail to Colonia 24 de Mayo, 2.5 km W on road from Puyo–Tena road at Km 9, 1°25′S, 77°58′W, *Stein & Tucker 3108* (MO). PERU. **Amazonas:** Prov. Bongara, 4 km N of Pomacocha on road to Rioja, 5°40′S, 77°22′W, *Knapp et al. 7497* (MO); Pomacocha, Vilcaniza, *Sagástegui 5997* (US); Mendoza, *Woytkowski 8236* (MO); hills 1–5 km SSE (150°) of Yambrasbamba, *Wurdack 1027* (US, photo NY). **Cajamarca:** Prov. Cutervo, distrito San Andrés, San Andrés–Chorro Blanco, El Suro, *Sánchez 317* (MO).

2. Hillia macrophylla Standley, Publ. Field Columbian Mus., Bot. Ser. 7: 201. 1931. TYPE: Ecuador. Chimborazo: base of Mt. Chimborazo, 900 m, June & Aug. 1860, *R. Spruce 6186* (holotype, K, photo K, F; isotype, F).

Hillia marcano-bertii Steyerm., Pittiera 9: 5. 1981. TYPE: Venezuela. Táchira: municipio Lobatera, Parque "Cazadero," carretera Palo Grande–Minas de Carbón de Lobatera, 6 Dec. 1979, *L. Marcano-Berti & I Peña 519-979* (holotype, VEN; isotype, MER not seen).

Suffrutescent herbs, shrubs, or small trees to 7 m tall; bark gray-brown to red-brown, smooth. Leaf blades elliptic to broadly elliptic-oblong or somewhat ovate, 9–22 cm long, 4.5–10 cm wide, acute to usually acuminate at apex with tip 5–10 mm long, cuneate to obtuse at base, chartaceous to coriaceous, sometimes pale abaxially; secondary veins pinnate, 6–8 pairs, midrib and secondary veins plane adaxially, prominent abaxially, sometimes with domatia; margins flat; petioles 6–20 mm long; stipules subtending flowers 22–76 mm long, 12–25 mm wide, sometimes becoming red. Flowers solitary; peduncles 1.5–2 mm long; bracts

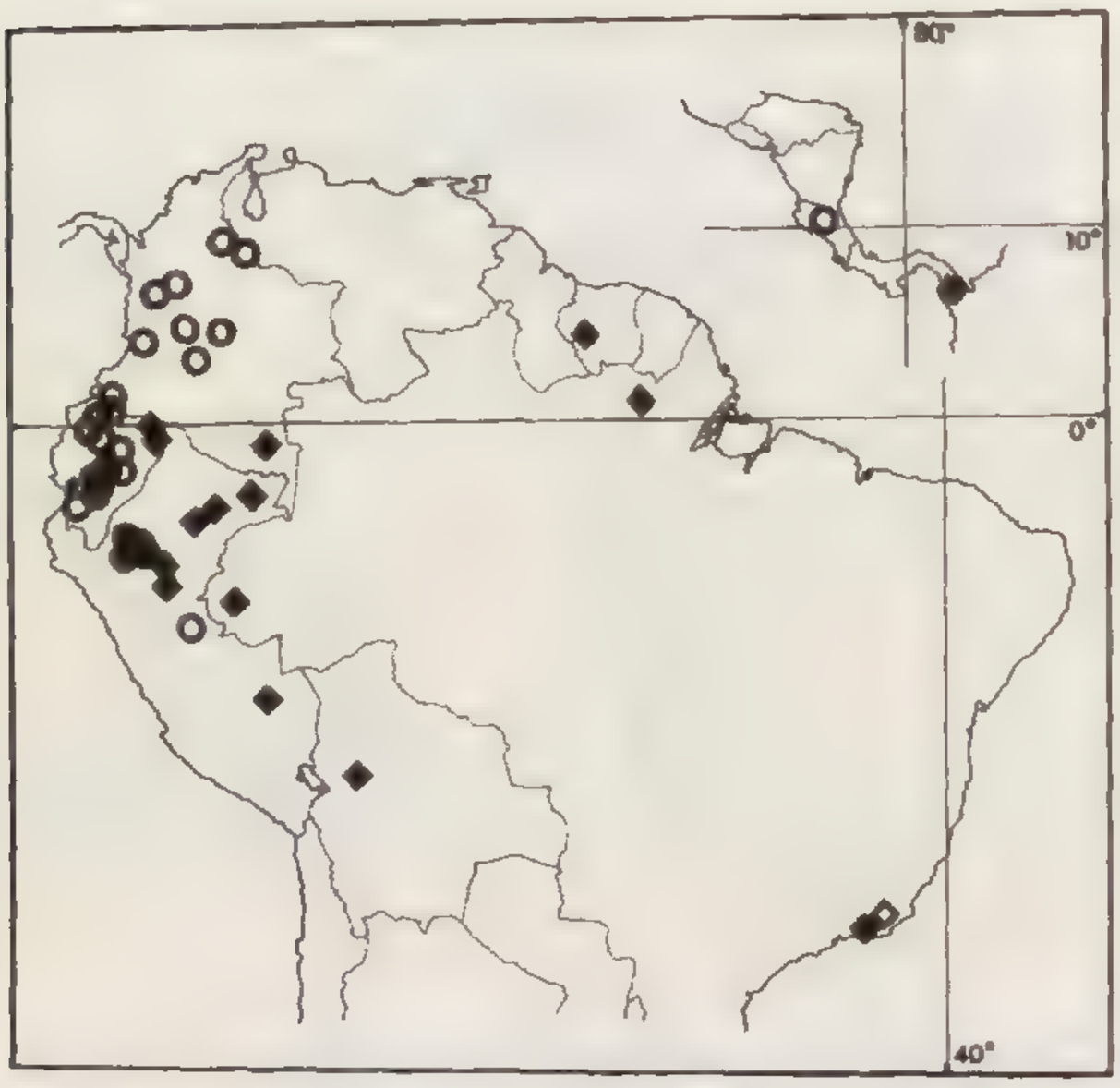

FIGURE 6. Distribution of *Hillia wurdackii* Steyerm. (solid circles), *H. macrophylla* Standl. (open circles), *H. ulei* K. Krause (solid diamonds), and *H. saldanhaei* K. Schum. (open diamond) in Central and South America.

lacking or 1.5–11 × 1.5–5 mm; calyx limb lacking; corolla salverform, white or pale green on surfaces exposed in bud, the tubes 85–112 mm long, the lobes 5–6, 35–54 mm long, 6–12 mm wide, triangular to narrowly triangular, acute; anthers 5–6(7), subsessile, ca. 8 mm long, with tips positioned 1–2 mm below top of corolla tube; ovary 5–10 mm long; stigmas subcapitate, 2–2.5 mm long, positioned immediately above anthers. Capsules 6.5–10 cm long including beak 1–5 mm long, 8–13 mm diam., not stipitate, smooth or with ca. 10 low longitudinal ribs; seeds 3–4 × ca. 1 mm, with trichomes 12–17 mm long. Figure 7C, D; Steyermark (1981: fig. 1, as *H. marcano-bertii*).

Habitat, phenology, and distribution (Fig. 6). Costa Rica, Venezuela, Colombia, Ecuador, and Peru, in wet forests at 800–1500 m. Collected in flower December to July and September to October, in fruit January, May, July to August, and November.

This species is distinguished by its large leaves and corollas. It is similar to *Hillia wurdackii*, *H. macromeris*, and *H. killipii* in its chartaceous to subcoriaceous leaves with the secondary veins prominent. Of these only *H. macromeris* has leaves of similar size, but it also has flowers about twice as large as those of *H. macrophylla*.

The only characteristics that would separate *Hillia marcano-bertii* are "pustulose" bark (which appears rather lenticellate in Steyermark's illus-

FIGURE 7. A, B. *Hillia macromeris* Standl. A. Habit with flower.—B. Flower opened near top of tube. C, D. *Hillia macrophylla* Standl.—C. Flower with stipule (floral).—D. Leaf. E–G. *Hillia macbridei* Standl.—E. Flower with stipule (floral).—F. Habit with capsule.—G. Stipule (vegetative). A, B, from *Lehmann BT 416* (NY); C, D, from *Jativa & Epling 285* (NY); E, from *Zak 3788* (MO); F, G, from *Schunke 436* (F). A–F to same scale, G to twice this scale.

tration), a "verrucose" abaxial leaf surface, and corolla lobes that are broader by about 3 mm. The corolla lobes of *Hillia* species may vary widely in size, and additionally are usually strongly rolled at anthesis, so their unrolled width is difficult to measure. The occurrence of pustulose bark and verrucose leaf surfaces in some specimens is well within the range of variation seen in other species of *Hillia*. A similar geographic disjunction is seen in other species of *Hillia*, e.g., *H. macrophylla*. Therefore, this species is not maintained here.

Representative specimens examined. COSTA RICA. **Puntarenas:** Upala, El Pilón, cabeceras del Río Celeste, 10°49′N, 84°57′W, *Herrera 1320* (MO). COLOMBIA. **Antioquia:** municipio Guatepe, ca. 8 km NNE of Guatepe, vereda Santa Rita, Finca Montepinar, 6°17′N, 78°08′W, *Zarucchi 4168* (MO). **Boyacá:** vertiente oriental de la cordillera Oriental, terraza a lo largo del río Sacameño, *Jarmillo & van der Hammen 2748A* (COL). **Chocó:** Quibdó-Medellín road, 59 km W of La Mansa, *Gentry & Rentería 24168* (COL, MO). **Cundinamarca:** al S de Santandercito, laguna de Catarnica, 40 km SO de Bogotá, *Uribe 3197* (COL, US). **El Valle:** Cordillera Occidental, vertiente occidental, hoya del río Dígua, río San Juan, abajo de Queremal a la derecha del río entre Kms 52–53, *Cuatrecasas 23963* (COL, F, US). **Meta:** Cordillera La Macarena, extremo NO, macizo Renjifo, *Irobo & Schultes 1059* (MO, US). **Nariño:** Reserva La Planada, 1°10′N, 77°58′W, *Restrepo 449* (MO), *de Benavides 9602* (MO), 1°05′N, 78°01′W, *Gentry et al. 60342* (MO). **Norte de Santander:** Cordillera Oriental, región del Sarare entre el Alto del Loroy y el Alto de Santa Inés, *Cuatrecasas et al. 12398* (F, GH). ECUADOR. **Azuay:** between Río Blanco and Río Norcay on road between Chacanceo and Molleturo, *Steyermark 52827* (F). **Cañar:** quebrada W of San Miguel near Hacienda Monte Negro, *Játiva & Epling 285* (NY). **Carchi:** environs of Chical 12 km below Maldonado on Río San Juan, 1°04′N, 78°17′W, *Madison et al. 4519* (F). **Cotopaxi:** 3 km E of El Palmar on Quevedo–Latacunga road, *Dodson & Gentry 10195* (MO). **El Oro:** 11 km W of Piñas on new road to Santa Rosa, *Dodson & Gentry 9136* (MO). **Imbabura:** Cordillera Occidental, trail to San Luis de la Vega, *Drew E-553* (NY, US). **Napo:** ridge SE of Chaco across Quijos River below Baeza, *Ownbey 2669* (F, US). **Pastaza:** trail to Colonia 24 de Mayo, 2.5 km W on road from main Puyo–Tena road at Km 9, 1°25′S, 77°58′W, *Stein & Tucker 3108* (MO). **Pichincha:** old Quito–Santo Domingo road, 2–9 km NE of turnoff to old road out of Alluriquín, 00°20′S, 78°55′W, *Luteyn et al. 8738* (AAU, CAS, NY). PERU. **Huánuco:** distrito Chinchao, Bosque Nacional de Iparia, a lo largo del río Pachitea cerca del campamento Miel de Abeja, cerca 20 km arriba de la confluencia con el río Ucayali, *Schunke 5247* (F).

3. **Hillia macromeris** Standl., Publ. Field Columbian Mus., Bot Ser. 7: 22. 1930. TYPE: Colombia. Cauca: forests of Santa María on Río Timbiquí, Sep. 1903, *F. C. Lehmann (Brother Thomas) 416* (holotype, NY, photos A, F; isotypes, F, K, photo of K sheet NY).

Shrubs or trees to 7 m tall or occasionally lianas; bark gray-brown to red-brown, smooth. Leaf blades elliptic to somewhat ovate, 10–19 cm long, 3–9 cm wide, acute to acuminate at apex with tip 1–2 cm long, cuneate to rounded at base, chartaceous to subcoriaceous; secondary veins pinnate, 5–8 pairs, midrib and secondary veins plane adaxially, prominulous to prominent abaxially, without domatia; margins flat; petioles 8–16 mm long; stipules 32–70 mm long, 7–13 mm wide. Flowers solitary; peduncles ca. 2 mm long; bracts lacking; calyx limb lacking; corollas salverform, white, the tubes 14.5–15 cm long, the lobes 6, 7.5–9 cm long, ca. 5 mm wide, very narrowly triangular, acute to attenuate; anthers 6, subsessile, 7–14 mm long, with tips positioned 12–15 mm below top of corolla tube; ovary 5–10 mm long; stigmas shortly linear, ca. 5 mm long, positioned immediately above anthers. Capsules ca. 11 cm long including beak 1–5 mm long, ca. 12 mm diam., not stipitate, smooth or with 8–10 low longitudinal ribs; seeds ca. 2 × 0.5 mm, with filaments ca. 10 mm long. Figure 7A, B.

Habitat, phenology, and distribution (Fig. 8). Colombia to Peru, in wet forests at 100–1890 m. Collected in flower in May, September, and November, in fruit in November.

This species is distinguished by its very long corolla tube and lobes, about 50% larger than those of any other species of *Hillia*. It is similar to *H. wurdackii*, *H. macrophylla*, and *H. killipii* in its chartaceous to coriaceous leaves with the secondary veins prominent on the abaxial surface. Of these only *H. macrophylla* has leaves of similar size, but it has flowers about half as large.

Additional specimens examined. ECUADOR. **Carchi:** along the Río Verde, at trail to Rafael's Mountain Finca, 0°52′N, 78°08′W, *Hoover 1920* (MO). **Morona-Santiago:** 6 km E of Limo on road (under construction) to La Unión, *Harling & Andersson 24490* (GB). PERU. **Amazonas:** near Shaim above Quebrada Nahim, 1 day's walk from Huampami, Río Cenepa, *Berlin 429* (MO). **Loreto:** Prov. Maynas, Yanamono, Explorama Lodge, 3°30′S, 72°50′W, *Vásquez & Jaramillo 4116* (MO). **San Martín:** Prov. Mariscal Cáceres, distrito Tocache Nuevo, Río de la Plata, NE of Tocache, *Schunke 8380* (MO).

4. **Hillia bonoi** Steyermark, Ernstia 42: 5. 1987. TYPE: Venezuela. Táchira: distrito Junín, entre Rubio y Las Delicias, 2000 m, 2 Apr. 1984, *J. Bono 3797* (holotype, VEN not seen, photo MO).

Shrubs to ca. 1 m tall; bark smooth, gray-brown to red-brown. Leaf blades broadly elliptic to somewhat ovate, 14.5–16.8 cm long, 9–10.8 cm wide,

acuminate at apex with tip 1–1.5 cm long, obtuse to rounded at base, stiffly subcoriaceous to coriaceous; secondary veins pinnate, ca. 10 pairs, midrib, secondary, and tertiary veins impressed adaxially, prominent abaxially, sometimes with domatia; margins flat to somewhat revolute; petioles 15–28 mm long; stipules subtending flowers ca. 38 × 12 mm. Flowers solitary, subsessile; bracts not seen; calyx limb not seen; corollas salverform, white, the tubes ca. 7 cm long, the lobes 5, ca. 3 cm long, ca. 1 cm wide, narrowly lanceolate to triangular, acute; anthers 5–6, subsessile, with tips positioned 2–3 mm below top of corolla tube; stigmas subcapitate, ca. 2–3 mm long, positioned immediately above anthers. Capsules not seen.

Habitat, phenology, and distribution. Known only from the type locality, in cloud forest at 2000 m. Collected in flower in April.

This species can be distinguished by its leaves, which are larger and proportionally wider than those of most other species of *Hillia*, with the secondary and higher-order venation impressed above and prominent on the lower surface.

5. Hillia killipii Standley, Publ. Field Columbian Mus., Bot. Ser. 8: 159. 1930. TYPE: Peru. Junín: Pichis trail between San Nicolás and Azupizu, 650–900 m, 6 July 1929, *E. P. Killip & A. C. Smith 26085* (holotype, F, photo F; isotypes, NY, US).

Shrubs or small trees to 5 m tall or sometimes lianas; bark of young twigs coppery red, papyraceous, and wrinkled in circumferential rings, becoming gray-brown and smooth or peeling on older stems. Leaf blades elliptic, 7.8–12.5 cm long, 3–5 cm wide, acuminate at apex with tip 5–10 mm long, acute to obtuse at base, chartaceous; secondary veins pinnate, 5–6 pairs, midrib and secondary veins smooth adaxially, prominent abaxially, without domatia; margins flat; petioles 8–17 mm long; stipules 17–27 mm long, 4–9 mm wide. Flowers solitary; peduncles 1–2 mm long; bracts lacking; calyx limb lacking; corollas salverform, white or pale green on surfaces exposed in bud, the tubes 53–80 mm long, the lobes 5–6, 33–48 mm long, 3–8 mm wide, narrowly triangular, acute; anthers 5, subsessile, 6–7 mm long, with tips positioned 6–7 mm below top of corolla tube; ovary 5–10 mm long; stigmas shortly linear, ca. 5 mm long, positioned immediately above anthers. Capsules 7–10 cm long including beak 1–5 mm long, ca. 8–10 mm diam., not stipitate, smooth or with ca. 10 low longitudinal ribs; seeds 2–5 × 0.8–1 mm, with filaments 10–25 mm long. Figure 5A, B.

Habitat, phenology, and distribution (Fig. 8). Peru and Ecuador, in wet forests at 600–1600 m. Collected in flower in January, April, and July to September, in fruit March, April, and July.

This species can be recognized by its chartaceous leaves with secondary veins prominent on the abaxial surface and coppery red, papery bark that is circumferentially wrinkled and sometimes peeling.

Representative specimens examined. ECUADOR. **Napo:** region of Archidona–Tena along Río Pano at foot of Cordillera de Guacamayos W of Tena, *Ownbey 2737* (F, US). PERU. **Cuzco:** Río Arasa NE of Cuzco, *Sandeman 3672* (F). **Loreto:** Pumayacu between Balsapuerto and Moyobamba, *Klug 3145* (A, F, GH, US). **San Martín:** Prov. Rioja, Pedro Ruíz–Moyobamba road, Km 390, 5°50′S, 77°45′W, *Smith 4385* (MO).

6. Hillia parasitica Jacquin, Enum. Pl. Carib. 18. 1760; Select. Stirp. Am. 96, t. 66. 1763. TYPE: Martinique, *Jacquin s.n.* (holotype, BM not seen; cited by Moore & Rendle, 1936).

Hillia longiflora Sw., Prodr. 58. 1788, nom. inval., pro syn.

Cosmibuena acuminata Ruiz & Pav., Fl. Peruv. 3: 4, t. 226. 1802. TYPE: Peru. Huánuco: Chicoplaya, 1798, *J. Tafalla 15/24* (holotype, MA not seen, photos F, GH, MO; isotype, F).

Saldanha nobilis Vell., Fl. Flum. 142. t. 3: 158. 1825. *Hillia parasitica* var *nobilis* (Vell.) Steyerm., Mem. New York Bot. Gard. 23: 292. 1972. TYPE: Brazil. Rio de Janeiro region, Fl. Flum. t. 3: 158, lectotype designated here.

Fereirea vellozoana Schult. & Schult. f., Syst. Veg. 7: 83. 1829. TYPE: Fl. Lusit. Bras. Spec. t. 1, fig. 8, 1788, lectotype designated here.

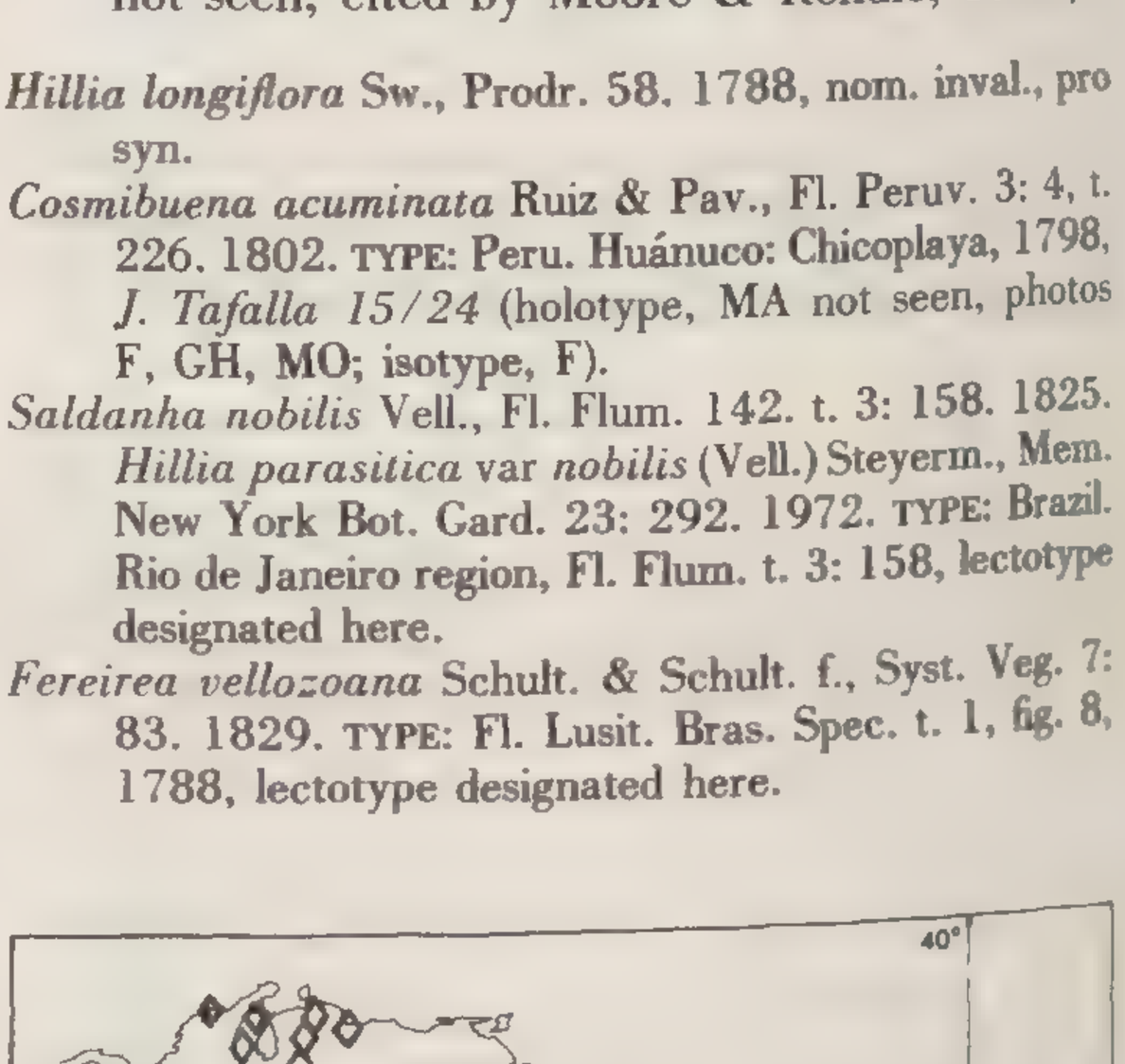

FIGURE 8. Distribution of *H. bonoi* Steyerm. (star), *H. macromeris* Standl. (solid circles), *H. killipii* Standl. (open circles), *H. macbridei* Standl. (solid triangles), *H. psammophila* Steyerm. (open triangle), *H. foldatsii* Steyerm. (solid diamond), and *H. costanensis* Steyerm. (open diamonds) in South America.

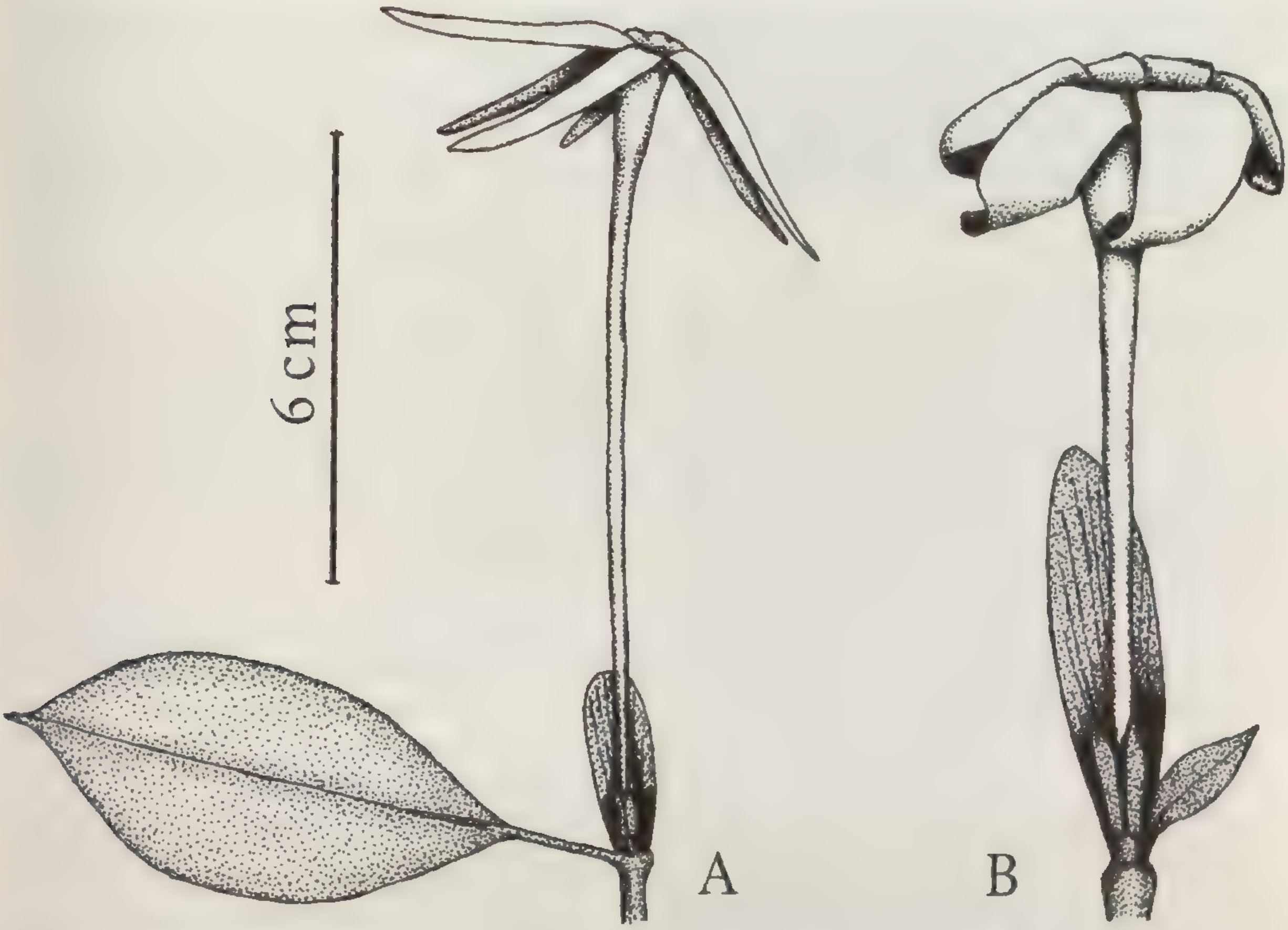

FIGURE 9. A, B. *Hillia parasitica* Jacq.—A. Habit with flower, "typical" form from the Antilles and eastern South America.—B. Habit with flower, "nobilis" form from northwestern South America. A, from *Otero 639* (MO); B, from *Stein & Cogollo 3564* (MO). A, B to same scale.

Hillia brasiliensis Cham. & Schltdl., Linnaea 4: 201. 1829. TYPE: Brazil. Brasilia aequinoctiali, *Sellow 1754* (holotype, B destroyed; isotypes, P, US).

Posoqueria montana Mart., Flora 24, Beibl. 2: 80. 1841. TYPE: Brazil. Minas Gerais: in sylvis montanis ad Villa Rica, April, *Oreas s.n.* (holotype, W not seen).

Hillia boliviana Britton, Mem. Torrey Bot. Club 3: 43. 1893. TYPE: Bolivia. Cochabamba: Yungas, 1890, *A. M. Bang 660* (holotype, NY; isotypes, F, GH, NY, US).

Hillia odorata K. Krause, Bot. Jahrb. Syst. 40: 321. 1908. TYPE: Peru. Junín: Prov. Tarma, prope Huacapistana, 1800 m, 14 Jan. 1903, *A. Weberbauer 2152* (holotype, B destroyed, photos F, GH, MO, NY; isotype, F).

Hillia weberbaueri Standl., Field Mus. Nat. Hist., Bot. Ser. 11: 214. 1936. TYPE: Peru. Without locality, 1909 1914, *A. Weberbauer 6955* (holotype, F, photo F).

Hillia maguirei Steyerm., Mem. New York Bot. Gard. 10(5): 209, fig. 73a–d. 1964. TYPE: Venezuela. Amazonas: Serranía Yutaje, Río Manapiare, Cerro Yutaje, 1750 m, 17–19 Feb. 1953, *B. Maguire & C. K. Maguire 35287* (holotype, NY; isotypes, GH, P not seen, US).

Hillia microcarpa Steyerm., Mem. New York Bot. Gard. 23: 292. 1972. TYPE: Venezuela. Mérida: steep NW- and NE-facing slopes above "La Isla," above Tabay, 2285 2745 m, 18 May 1944, *J. A. Steyermark 56591* (holotype, F, photo NY).

Suffrutescent herbs, shrubs, or small trees to 8 m tall; bark gray-brown to red-brown, smooth. Leaf blades elliptic to elliptic-oblong, 3.4–13 cm long, 1.7–6.5 cm wide, acute to usually acuminate at apex with tip 5–10 mm long, cuneate to acute at base, subcoriaceous to coriaceous; secondary veins pinnate, (2–)4–8(–9*) pairs, plane or sometimes midrib prominulous abaxially, without domatia; margins flat; petioles (2–)4–22 mm long; stipules 9–55 mm long, 4–14 mm wide, sometimes red. Flowers solitary; peduncles 1–4 mm long; bracts lacking or 2–7(–9*) × 1–4 mm; calyx limb lacking or divided to base, the lobes (5–)6(–9), 3–12 mm long, 0.8–6 mm wide, narrowly triangular to ligulate or orbicular, acute to rounded; corollas salverform, white or sometimes pale green or pink on surfaces exposed in bud, the tubes (38*–)60–125 mm long, the lobes (5–)6, 15–60 mm long, 4–12 mm wide, triangular to lanceolate, obtuse to acute; anthers (5–)6, subsessile, 4.5–8 mm long, with tips positioned 2–3 mm below top of corolla tube; ovary 5–10 mm long; stigmas subcapitate, 1–2 mm long, positioned immediately above anthers. Capsules 3–11.5(–20) cm long including beak 1–5 mm long, 6–10(–12*) mm diam., not stipitate, smooth; seeds 2–4 × 0.5–1 mm, with filaments 8–15 mm long. Figure 9; Andersson & Persson (1991: fig. 2C,

D); Howard (1989: fig. 188); Lamarck (1792: t. 257, fig. 1); Moore & Rendle (1936: fig. 3); Robbrecht (1988: figs. 58, 59); Roemer (1796: t. 6, fig. 8); Sastre & Portecop (1985: fig. 220); Schumann (1889: fig. 111; 1891: fig. 19P–R); Sims (1804: fig. 721); Steyermark (1974: fig. 21); Swartz (1791: t. 5, fig. 1).

Habitat, phenology, and distribution (Fig. 10). Throughout the Antilles and most of mainland tropical South America, in wet forests at 200–2400 m. Collected in flower and in fruit throughout the year.

This species is common and variable. It is distinguished by its leaf blades with acute to usually acuminate apices and the secondary venation plane and usually not evident, and usually 6-merous corollas with tubes 60–125 mm long and lobes 15–60 mm long. Measurements cited by Steyermark (1972, 1974) but not observed on material studied are designated with asterisks (*) in the description above.

Hillia parasitica varies in several features that seem uncorrelated with geographic distribution. Leaf size may vary even on a single plant, but in general appears to be correlated with habitat: plants from wet windy ridges and high montane areas tend to have smaller leaves than plants from lower, drier, or more sheltered sites. The venation is usually plane, although the midrib may be prominulous abaxially in plants from South America, particularly on relatively large leaves. Secondary venation is more evident on some collections than others, apparently due as much to treatment of the specimens with formalin or alcohol as to any inherent feature of the plants.

The shape of the corolla lobes in *Hillia parasitica* varies from narrow in the Antilles and northeastern South America to relatively broad in the southwestern part of its range, but the variation is continuous and does not appear to be correlated with any other feature. The lengths of the corolla tube and lobes also vary, but within-population ranges are frequently as wide as differences among plants from widely different sites. Plants from the tops of tepuís tend to have relatively shorter corollas, but these do not fall outside the range of corolla size represented in other areas. Occasional plants from both the Antilles and the mainland lack a calyx limb, as do other species of *Hillia*. Tepuí plants with relatively short corollas and no calyx limb were segregated by Steyermark as *H. maguirei*, but when the collection locality is not known these plants cannot be segregated and this species is not maintained here. When present, the calyx

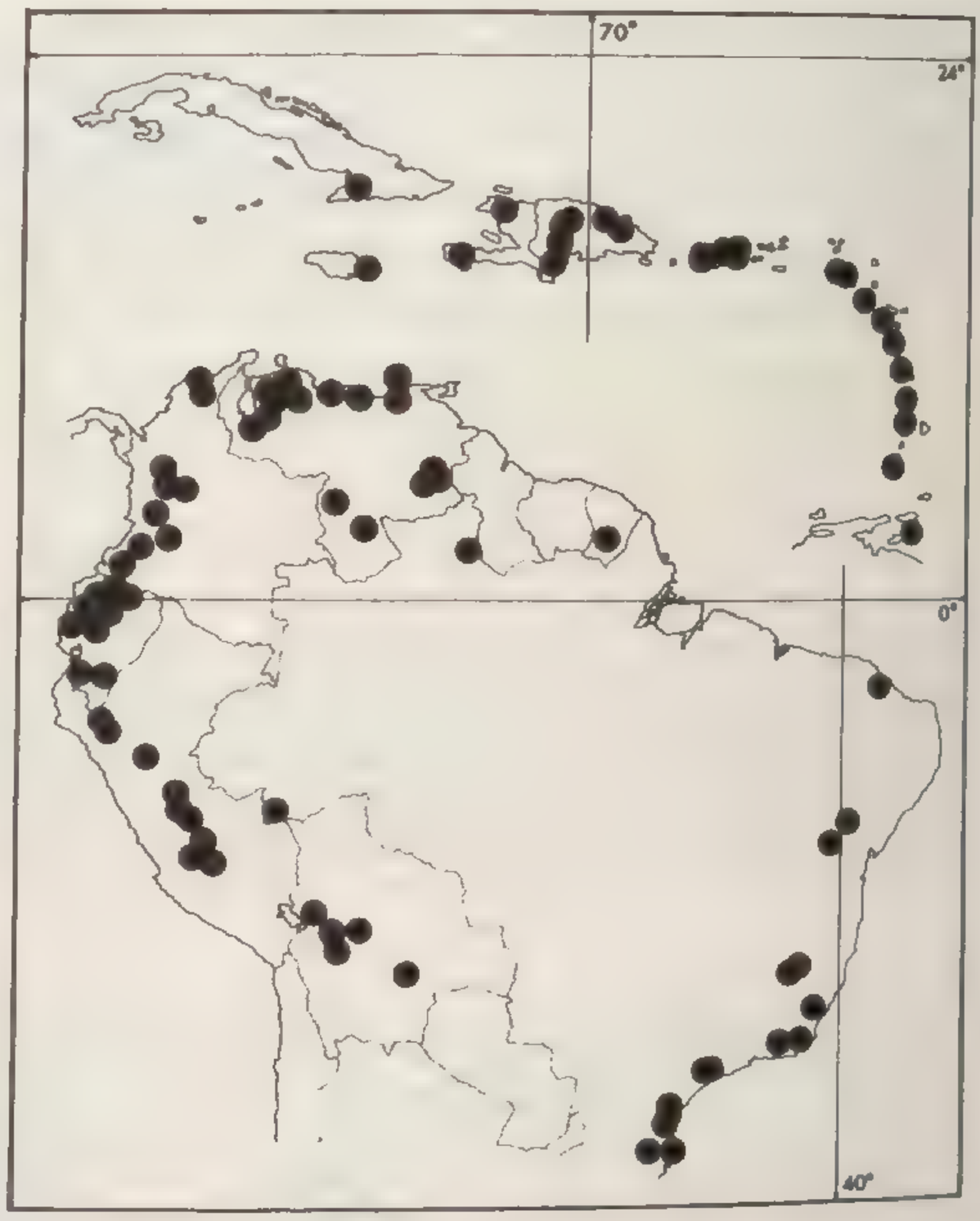

FIGURE 10. Distribution of *Hillia parasitica* Jacq. (solid circles) in the Antilles and South America.

lobes in *H. parasitica* vary in shape from triangular to elliptic throughout most of the geographic range, to broadly ligulate or orbicular in some plants from scattered localities in Amazonian Venezuela and Colombia. Steyermark segregated plants with broadly ligulate to orbicular calyx lobes as *H. microcarpa*, based on both this feature and relatively small flowers. However, comparable variation in the shape of the calyx lobes is seen in other species of *Hillia* from several subgenera, and the flowers fall within the normal range for *H. parasitica*. No other features distinguish *H. microcarpa*, and it is not maintained here.

The stipules subtending the flowers range in length from 14 to 30 mm in the Antilles, from 15 to 40 mm in northern and eastern South America, and from 25 to 74 mm in western South America. Plants of western South America with relatively long floral stipules that tend to persist until anthesis have been segregated as *Hillia boliviana*. However, the size range for the floral stipules of "*H. boliviana*" overlaps that found in plants from elsewhere, as does the degree of persistence, and this species is not maintained here.

Steyermark (1972) recognized two varieties of *Hillia parasitica*, variety *parasitica* and variety *nobilis*, based on corolla size, size of the stipules subtending the flowers, and form of the bracts ("bracteoles"). He gave the range of variety *nobilis*

as "southern Brazil, Bolivia, Colombia, and possibly Peru," with the typical variety occupying a more or less complementary range in the "Lesser and Greater Antilles, Mexico, Central America, and South America (Venezuela and Territorio Roraima, Brazil)." Unfortunately, the range of corolla and bract sizes he gave for variety *nobilis* also includes many Antillean plants, while the form of the bracts he attributed to variety *parasitica* does not fit most Antillean plants, and several of the measurements he gave for these taxa are contradicted in specimens that he annotated contemporaneously. The characters he used to separate these varieties do indeed vary over the geographic range of *H. parasitica*, but appear to do so independently. Examination of specimens he annotated suggests that the relatively broad corolla lobes found in plants from the southwestern part of the range of *H. parasitica* were probably the primary character used in practice to delimit variety *nobilis*. This variation in corolla lobe shape is continuous and uncorrelated with other characteristics; variety *nobilis* is not recognized here.

Hillia parasitica is weedy and common in the Antilles, where it may be epiphytic or rooted in saturated disturbed soils. It is also commonly collected in southeastern Brazil, but relatively few collections have been seen from Colombia, Ecuador, and Bolivia. Howard has suggested in notes accompanying specimens from Puerto Rico that there may be some incidence of "distyly or cryptic dioecy," but this has not been tested. His specimens show variation by several millimeters in the position of the stamens relative to the top of the corolla tube, similar to the variation found in other species, but the stigmas are held above the anthers in all specimens seen. The flowers are very strongly and sweetly fragrant during the night, beginning at about 6–7 P.M. in Puerto Rico, but are odorless during the day.

Representative specimens examined. BOLIVIA. **Cochabamba:** small power station ca. 80 mi. NE of Cochabamba, *Brooke 6700* (F, NY). **La Paz:** Prov. Murillo, 44 km below Lago Zongo dam, vicinity of Cahua hydroelectric plant, 16°03′S, 68°01′W, *Solomon 10826* (CTES, MO). **Santa Cruz:** Santa Cruz, *Williams 1478* (F, NY, US). BRAZIL. **Bahia:** summit of Morro do Chapeu, ca. 8 km SW of town of Mdoch to W of road to Utinga, 11°35′S, 41°12′W, *Harley 22773* (NY, US). **Ceará:** sitio Espírito Santo, Serra da Aratanha–Maranguapé, *Martens & Castro 7076* (MO). **Espirito Santo:** Santa Leopoldina, cabeceira do Río Bonito, divida com o municipio de Santa Teresa, *Boudet 2280* (MO). **Minas Gerais:** mpio. Sêrro, Boca de Mata, *Williams & Assis 7916* (F, GH). **Paraná:** Tacarchí, *Dusén 16113* (A, F, GH, MO, NY). **Rio de Janeiro:** region of Itatiaia, *Ginzberger 273* (F), *Hoehne 11504* (F), *Plowman 2862* (GH). **Roraima:** summit of Serra de Lua, 2°25–29′N, 60°11–14′W, *Prance et al. 9436* (F, NY). **Santa Catarina:** Mina Velha, Garura, San Francisco do Sul, *Reitz & Klein 5789* (NY, US). **São Paulo:** Boracéa, Salisópolis, *Kuhlmann & Kühn 1750* (F). COLOMBIA. **Antioquia:** Cordillera Central 7–15 km E of Sonsón on road to Nariño, 5°43′N, 75°15′W, *Stein & Cogollo 3564* (COL, MO, NY). **Boyacá:** extreme western part of Mt. Chapón, *Lawrance 351* (F, MO, NY). **Cauca:** La Depresión, foot of Cerro Pinche, *Core 1327* (US). **Cundinamarca:** Cordillera Oriental, municipio San Bernardo, verde de Santa Rita, Alto de Buenos Aires, *Jaramillo et al. 7072* (COL). **Huila:** Cordillera Oriental, E of Neiva, *Rusby & Pennell 863* (NY). **Magdalena:** Sierra Nevada de Santa Marta, SW of Finca Los Arroyitos, 10°56′N, 73°58′W, *Kirkbride 2398* (COL, NY, US). **Nariño:** entre Altaquer y Junín, Cuyambe, *Idrobo 2356* (NY, US). **Santander:** Virolín a Charaló, *Romero & Jaramillo 6753* (COL). CUBA. **Granma:** Río Guayabo above the falls, *Shafer 3619* (F, NY, US). DOMINICA. Near Freshwater Lake and Laudat, *Smith 10256* (A, NY, US), *Wilbur et al. 7389* (F, MO, NY). DOMINICAN REPUBLIC. **Barahona:** al S de Baoruco, 4 km arriba del poblecito rural "Entrada de Cortico," en el camino al Gajo ("monteado Nuevo"), 18°07′30″N, 71°13′30″O, *Zanoni et al. 18867* (NY). **El Seibo:** Los Haitises, cerca de la caseta de guardaparques en Monte Bonito, 19°00′N, 69°30′W, *Zanoni et al. 35437A* (NY). **La Vega:** Bonao, subido al Casabito, *Liogier & Liogier 21526* (F, NY, US). **Peravia:** 14.2 km al N del Parque Central en San José de Ocoa en el camino a Carmena, zona rural "El Caliche," 18°37′N, 70°31′W, *Zanoni et al. 19853* (NY). **Samaná:** vicinity of Laguna, Samaná Peninsula, chiefly on Pilón de Azúcar, *Abbott 2357* (GH). **Santiago:** Cordillera Septentrional, Loma Diego de Ocampo, 19°34′30″N, 70°44′30″W, *Zanoni et al. 26660* (NY). ECUADOR. **Carchi:** just below Tambo Bella Vista, pass between Río San Juan and Río Plata, *Steere 8070* (F). **El Oro:** along trail between Portovelo and Río Cabra, passing Minas Nuevas and Huertas and arriving at Cachicarán, *Steyermark 54093* (A, F). **Imbabura:** Río Lita below Buenos Aires, Cordillera Occidental, *Steere & Camp 8196* (F). **Manabí:** San Sebastián, Machalilla National Park, 1°36′S, 80°42′W, *Gentry et al. 72567* (MO). **Pichincha:** km 70, old road from Quito to Santo Domingo, *Dodson & Dodson 11852* (MO). **Morona–Santiago:** Plan del Milagro, ca. 10 km NW of Indanza, *Jørgensen 40* (F). **Sucumbíos:** road in construction between Santa Bárbara and La Bonita, *Harling & Andersson 12475* (US). **Tungurahua:** northern slopes of Volcán Tungurahua, *Dodson & Thien 1875* (MO). FRENCH GUIANA. **Cayenne:** Montagnes de la Trinité, sommet nordest, *de Granville 5856* (MO, NY), *6215* (MO). GRENADA. Morne Quaqua, *Beard 1225* (A, F, GH, MO, US). GUADELOUPE. Trois-Rivières, *Duss 2546* (F, NY, US). HAITI. **Nord:** Massif du Nord, Anse-a-Faleur, Morne Chêneau, *Ekman 4405* (GH, NY, US). **Sud:** Montagne de la Hotte, summit Morne Delour, *Eyerdam 393* (GH, US). JAMAICA. **Surrey:** vicinity of Cinchona, near Vinegar Hill, *Britton 219* (F, NY). MARTINIQUE. Deux-Chounde du Lorrain, Mont Pelée, *Père Duss 1462* (F, NY, US). MONTSERRAT. Summit of Castle Peak, English Crater, central mountain range, *Howard & Howard 17553* (A). PERU. **Amazonas:** Prov. Bagua, 12 km E of La Peca, *Barbour 2614* (MO). **Ayacucho:** Prov. Huamango, Tambillo, *de Jelski 367* (MO). **Cuzco:** Prov. La Convención, 10 km walking NE from Hacienda Luisiana and the Apurimac River,

12°30′S, 73°30′W, *Dudley 10414* (F). **Huánuco:** ditto. Chinchao, camino a la Hacienda Derrepente, margen derecha del río Derrepente, *Schunke V. 5317* (COL, F, GH, NY, US). **Junín:** Chanchamayo valley, *Schunke 290* (F). **Loreto:** Divisoria, *Ferreyra 1666* (US), *2255* (US). **Pasco:** Prov. Oaxapampa, Río Chontabamba valley, 1–15 km from Oxapampa, 10°35′S, 75°30′W, *Smith 4139* (MO). **San Martín:** Prov. Mariscal Cáceres, Tocache Nuevo, río de la Plata, *Schunke V. 8170* (F, MO). PUERTO RICO. E slope of Luquillo Mountains, *Heller 4612* (A, F, GH, MO, NY, US); Cayey, Rte. 184, Cerro la Santa in Carite Reserve, *Taylor 6353* (UPRRP); Barranquitas, Cerro Torrecilla, *Alvarez & Rodríguez 24* (UPRRP); Mount Mandios near Jayuya, *Britton & Cowell 924* (F, NY); Monte Alegrillo, near Maricao, *Britton et al. 2591* (NY, US). SABA. Top of the mountain, *Arnoldo 3302* (A). ST. KITTS. Molyneaux Estate, *Britton & Cowell 697* (NY, US). ST. LUCIA. Gros Piton, *Beard 1163* (F, GH, MO, US). ST. VINCENT. Mount St. Andrews, *Eggers 6754* (A, US). TRINIDAD. Aripo road via Arima near bathing pool, Mile Posts 4, 5, *Broadway 5709* (F, MO). VENEZUELA. **Amazonas:** dept. Atabapo, slopes of Marahuaca, 1–2 km N of Sima Camp, 3°43′N, 65°31′W, *Liesner 18431* (MO, NY). **Aragua:** Pica hacia Cerro Periquitos, estación biológica Rancho Grande, *Aristeguieta 4239* (F, MO). **Bolívar:** Auyantepuí, *Cardona 207* (F, US), *Steyermark 93882* (NY), *94089* (NY), *Vareschi & Foldats 4771* (F). **Falcón:** ditto. Petit, Sierra de San Luis, Paraguariba, 3 km ENE of Cerro Galicia, 2 3 km N of Curimagua, 11°11′30″N, 69°41′W, *Plowman et al. 13370* (F). **Lara:** Parque Yacambú, beyond crest from Sanare, *Berry 3468* (MO). **Mérida:** between La Azulita and La Trampa on road to Lagunillas, *Steyermark 56156* (F). **Miranda:** Cerro del Bachiller, near E end, above Quebrada Corozal, S of Santa Cruz, 10 km by air W of Cúpira, 10°09′N, 65°48′W, *Steyermark & Davidse 116874* (MO). **Monaguas:** ditto. Acosta, serranía del Turumiquire, altiplanicie en la fila La Montaña, cabeceras del río Negro (afluente del río Colorado), 10°02′N, 63°52′O, *Huber et al. 6316* (NY, US). **Nueva Esparta:** Isla Margarita, San Juan Mountain, *Johnston 41* (F, GH, NY, US). **Portuguesa:** 50 km WNW of Guanare by air, 15-17 km N of Chabasquén, 9°28′N, 69°55′W, *Liesner et al. 12775* (MO). **Yaracuy:** 10 km N of Salom, top of Gamoletal, El Amparo, *Davidse et al. 20716* (MO, NY).

2. Hillia subg. **Andinae** C. M. Taylor, subg. nov. TYPE: *Hillia macbridei* Standl.

A *Hillia* subg. *Hillia* stigmatibus linearibus corolla infra medium positis differt.

Calyx limb divided to base, lobes 5–6; *corollas* carnose, salverform, white, lobes 5–6; *stamens* 5–6, attached near middle of corolla tube; anthers subsessile; *stigmas* linear, positioned below anthers.

One species, Ecuador to central Peru.

7. Hillia macbridei Standley, Publ. Field Columbian Mus., Bot. Ser. 4: 277. 1929. TYPE: Peru. Junín: Hacienda Schunke, La Merced, ca. 4000 ft. [1290 m], 27 Aug.–1 Sep. 1923, *J. F. Macbride 5670* (holotype, F, photos F, NY).

Suffrutescent herbs or shrubs to 1 m tall; bark gray-brown to red-brown, smooth. Leaf blades lanceolate, 1.8–3 cm long, 4–8 mm wide, acute at apex, rounded at base, coriaceous to usually stiff; secondary veins obscure, smooth or midrib sometimes prominulous abaxially, without domatia; margins frequently revolute; petioles 1–4 mm long; stipules 8–20 mm long, 1.5–6 mm wide. Flowers solitary; peduncles 1–1.5 mm long; bracts lacking or 1–2 mm long and wide; calyx limb divided to base, the lobes 5–6, triangular to lanceolate or elliptic, 1–5 mm long, 0.5–3 mm wide; corollas salverform, white, the tube 40–49 mm long, 1.5–2.5 mm diam., the lobes 5–6, 22–24 mm long, 2.5–4 mm wide, narrowly triangular to linear, acute; anthers 5–6, subsessile, 3.5–5 mm long, with tips positioned 2–3.5 mm below top of corolla tube; ovary 3–4 mm long; stigmas 2–4 mm long, linear, positioned below anthers. Capsules 4–6 cm long including beak ca. 1 mm long, 7–8 mm diam., with stipes 3–7 mm long, smooth or with ca. 8 longitudinal lines or low ridges; seeds ca. 3 × 1 mm, with filaments ca. 1 cm long. Figure 7E–G.

Habitat, phenology, and distribution (Fig. 8). Ecuador to central Peru, in wet forests at 1300–1700 m. Collected in flower in September, in fruit August to October.

This species is distinguished by its relatively small, usually stiff, lanceolate leaf blades with the margins frequently revolute. The flower is described for the first time here.

Additional specimens examined. ECUADOR. **Napo:** Cantón Archidona, faldas al S del volcán Sumaco, comunidad El Pacto 9 km al N de la carretera Hollín–Loreto, sector Guagua Sumaco, 00°40′S, 77°35′W, *Zak & Jaramillo 3788* (MO). PERU. **Junín:** Hacienda Schunke above San Ramón, *Schunke A100* (F); Chanchamayo Valley, *Schunke 436* (F).

3. Hillia subg. **Tetrandrae** C. M Taylor, subg. nov. TYPE: *Hillia tetrandra* Sw.

A subgeneribus ceteris *Hilliae* corollaris hypocrateriformibus 4-lobatis et stigmatibus linearibus infra medium positis differt.

Calyx limb lacking or with lobes 4; *corollas* carnose, salverform, white or sometimes pale green on surfaces exposed in bud, lobes 4; *stamens* 4, attached near top of corolla tube; anthers subsessile; *stigmas* linear, positioned below middle of corolla tube.

Five species in the Greater Antilles, Mexico, Central America, and northeastern South America.

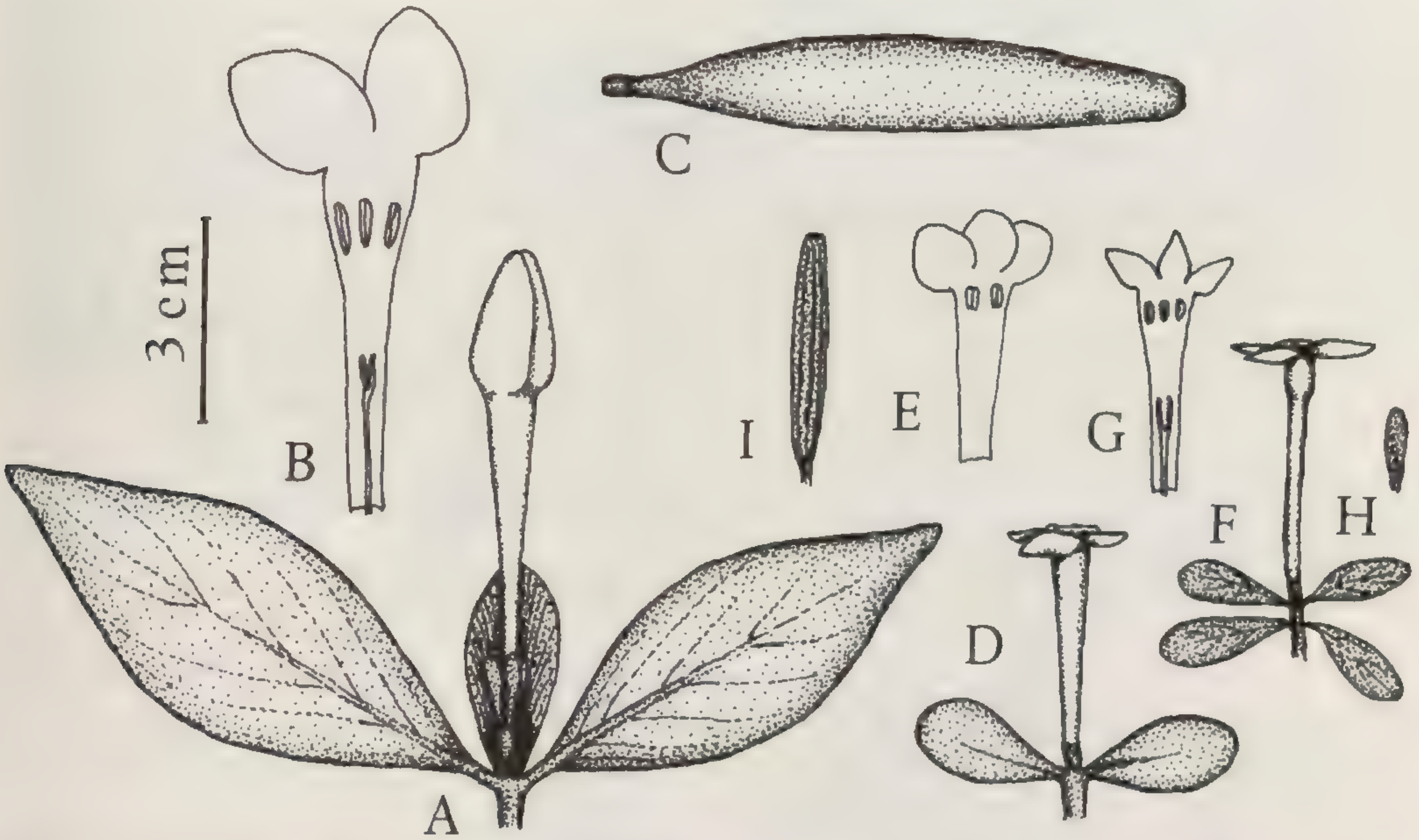

FIGURE 11. A–C. *Hillia loranthoides* Standl.—A. Habit with flower.—B. Flower opened.—C. Capsule. D, E. *Hillia palmana* Standl.—D. Habit with flower.—E. Corolla opened. F–I. *Hillia panamensis* Standl.—F. Habit with flower.—G. Flower opened.—H. Stipule (floral).—I. Capsule. A, from *Breedlove 57488* (F); B, from *Brenes 3839* (F); C, from *Williams 41950* (F); D, E, from *Wilbur 19782* (F); F, G, H, from *Dressler 1487* (NY). A–G to same scale, H to twice this scale.

8. Hillia loranthoides Standley, J. Wash. Acad. Sci. 18: 165. 1928. TYPE: Costa Rica. Guanacaste: Quebrada Serena SE of Tilarán, ca. 700 m, 27 Jan. 1926, *P. C. Standley & J. Valerio 46152* (holotype, US, photo F).

Hillia macrocarpa Standl. & Steyerm., Publ. Field Mus. Nat. Hist., Bot. Ser. 23: 23. 1943. TYPE: Guatemala. Quezaltenango: lower S-facing slopes of Volcán Santa María between Santa María de Jesús and Calajuache, along great barranca between Finca Pirineos and San Juan Patzulin, 1300–1500 m, 6 Jan. 1940, *J. A. Steyermark 33667* (holotype, F, photo F).

Suffrutescent herbs or shrubs to 1.5 m tall; bark gray-brown, smooth. Leaf blades elliptic to somewhat oblanceolate, 2–10 cm long, 1.6–4.5 cm wide, acute to sometimes acuminate at apex with tip 3–5 mm long, cuneate to attenuate at base, coriaceous and usually thickly so; secondary veins pinnate, 3–5 pairs, plane, without domatia; margins flat; petioles 5–15 mm long; stipules 15–34 mm long, 8–14 mm wide. Flowers solitary; peduncles 1–4 mm long; bracts lacking or 1–3 × 1–2 mm; calyx limb lacking or divided to base, the lobes 4, 5–10 mm long, 1–4 mm wide, ligulate to oblanceolate, acute; corolla salverform, white, the tube 45–75 mm long, the lobes 4, 15–25 mm long, 10–24 mm wide, elliptic, rounded; anthers 4, 7–8 mm long, subsessile, with tips positioned 5–8 mm below top of corolla tube; ovary 3–10 mm long; styles 13–15 mm long; stigmas 8–12 mm long, linear, positioned below middle of corolla tube. Capsules 30–75 mm long including a beak 1–3 mm long, 5–11 mm diam., without stipes, smooth; seeds 1.5–4 × ca. 0.5–1 mm, with filaments 6–13 mm long. Figure 11A–C.

Habitat, phenology, and distribution (Fig. 12). Southern Mexico to northern Guatemala and northern to central Costa Rica, in wet forests at 700–2700 m. Collected in flower December to June, in fruit in January, March, and May.

This species differs from *Hillia tetrandra* and *H. maxonii* in its acute or shortly acuminate, usually very thickly coriaceous leaf blades. It may represent an acute-leaved variant of *H. maxonii*. Aside from geographic range, no features separate the plants of Mexico and Guatemala described as *H. macrocarpa* from those of Costa Rica, and this name is placed in synonymy here. The resultant apparently disjunct range of this species is similar to that of *H. panamensis* and some species of *Psychotria* (Hamilton, 1989). The report of *H. triflora* from southern Mexico (Taylor, 1989) was a misidentification of *H. loranthoides*.

FIGURE 12. Distribution of *Hillia loranthoides* Standl. (upper map) and *H. panamensis* Standl. (lower map) in southern Mexico and Central America.

Representative specimens examined. COSTA RICA. **Alajuela:** La Palma de San Ramón, *Brenes 3839* (CR, F), *3847* (CR, F), *5439* (CR, F, NY), *6137* (CR, F), *Lent 1692* (CR, F). **Cartago:** El Retiro, Santa Cruz de Turrialba, *Valerio 1359* (CR). **Puntarenas:** San Luis River valley 1.5 km upstream from San Luis village, *Haber & Hammel 1787* (CR, MO). GUATEMALA. **Baja Verapaz:** Sierra de las Minas ca. 5 km S of Purulha, 1600 m, *Williams et al. 41950* (F). **Huehuetenango:** km 332 of the Panamerican Hwy. 5 km E of the Mexican border at La Mesilla, *Iltis & Lind G202* (WIS). **Quezaltenango:** Quezaltenango, 2666 m, *Vaught 305* (US). MEXICO. **Chiapas:** municipio La Trinitaria, 10 km ENE of Dos Lagos above Santa Elena, 1170 m, *Breedlove & Almeda 57488* (CAS, NY). **Oaxaca:** vicinity of Concordia, Montecristo, 1100 m, *Makrinus 727* (US).

9. Hillia tetrandra Swartz, Prodr. 58. 1788. TYPE: Jamaica. Coldspring, *O. Swartz s.n.* (holotype, S not seen; isotype, BM not seen, photo NY).

Hillia tuxtlensis Sessé & Mociño ex DC., Prodr. 4: 351. 1830, nom. inval., pro syn.

Suffrutescent herbs or shrubs to 4 m tall; bark gray-brown, smooth. Leaf blades obovate to elliptic, 3–7.5(–10) cm long, 1–3(–4.5) cm wide, obtuse to usually rounded at apex, attenuate at base, subcoriaceous to coriaceous; secondary veins pinnate,

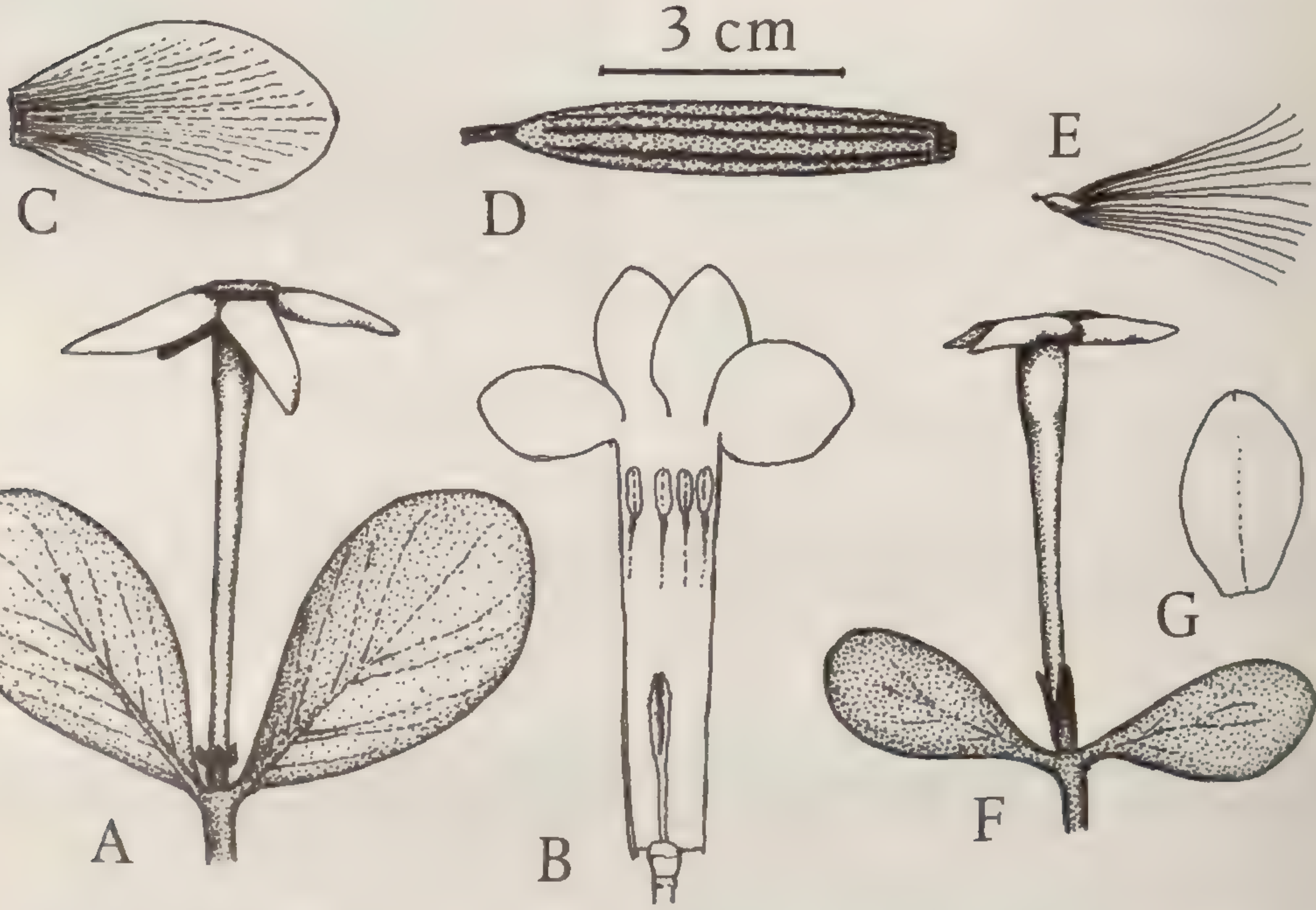

FIGURE 13. A–E. *Hillia tetrandra* Sw.—A. Habit with flower.—B. Flower opened.—C. Stipule (floral).—D. Capsule.—E. Seed. F, G. *Hillia maxonii* Standl.—F. Habit with flower.—G. Stipule (floral). A, B, from *Chazaro 3380* (F); C, D, E, from *Menéndez L. 85* (F); F, G, from *Maxon et al. 7501* (US). A–D, F to same scale, E to three times this scale, G to twice the first scale.

FIGURE 14. Distribution of *Hillia tetrandra* Sw. in southern Mexico, Central America, and the Greater Antilles.

3–5(–6) pairs, plane, without domatia; margins flat; petioles 1–11 mm long; stipules 8–30 mm long, 5–20 mm wide. Flowers solitary; peduncles 1–5(–10) mm long; bracts lacking or 3–4 × 1–2 mm; pedicels 0–3 mm long; calyx limb lacking or divided to base, the lobes 4, 7–19 mm long, often unequal, 1–3(–5) mm wide, oblanceolate to ligulate, rounded; corollas salverform, white, the tube 25–78 mm long, the lobes 4, 10–27 mm long, 8–22 mm wide, elliptic to broadly elliptic, broadly rounded; anthers 4, subsessile, 4.5–5 mm long, with tips positioned 2–3 mm below top of corolla tube; ovary 5–10 mm long; styles 8–18 mm long; stigmas 7–11 mm long, 2–3 mm wide, flattened, linear, positioned below middle of corolla tube. Capsules 25–80 mm long including a beak 1–3 mm long, 5–9 mm diam., not stipitate, with ca. 8 rounded to winged longitudinal ridges to 1 mm high; seeds 2.5–3.5 × 1–1.5 mm, with filaments 8–17 mm long. Figure 13A–E; Standley & Williams (1975: fig. 14).

Habitat, phenology, and distribution (Fig. 14). Cuba, Jamaica, Hispaniola, and southern Mexico to northern Nicaragua, in moist to wet, usually rocky forests at 0–1350(–2650) m. Collected in flower March to November, in fruit throughout the year.

This frequently collected species is characterized by its rounded, usually subcoriaceous leaf blades and ridged capsules. Leaf size in plants from Belize and Honduras is frequently markedly larger than in plants from other areas. Some individual plants from Guatemala, Belize, and Mexico lack a calyx limb; there is no intermediate stage with reduced lobes. This sporadic absence of a calyx limb is found in other *Hillia* species and does not appear to be of taxonomic significance. The corollas vary by as much as 100% in size on material studied, although this may be largely due to shrinkage in dried specimens.

Hillia tetrandra is similar to *H. maxonii* of southern Nicaragua to Colombia. The latter can be separated by its smooth to only very slightly ridged capsules and thickly coriaceous leaf blades with the secondary veins usually not discernible. Specimens that lack capsules may be difficult to separate, particularly in Nicaragua where the species occur together. These two species appear to differ ecologically: plants of *H. tetrandra* are generally found below 1000 m in moist formations, while *H. maxonii* is usually reported from very wet forests on ridgetops above 800 m, or from coastal mangrove formations.

Representative specimens examined. BELIZE. **El Cayo:** Mt. Pine Ridge, banks of Río On, *Lundell 6799* (F, GH, NY, US). **Stann Creek:** Middlesex, *Gentle 3006* (MO, NY). **Toledo:** Río Grande, *Schipp S-585* (A, F, GH, MO, NY). CUBA. **Cienfuegos:** Buenos Aires, *Roig & Acuña 6104* (NY). **Granma:** Pico Turquino, Loma Cordero, *Bucher 47* (NY). **Guantánamo:** near Laguna del Galano, Toa, *Alain 3856* (GH). **Las Villas:** Trinidad Mountains, near El Naranjo, *Webster et al. 209* (A). **Pinar del Río:** Rangel, Rosario Mountains, *Alain 6034* (GH, NY). **Santiago de Cuba:** Gran Piedra, *Clemente 7144* (GH, US). **Villa Clara:** Las Lagunas, Buenos Aires,

Jack 6812 (A, DS, F, NY). DOMINICAN REPUBLIC. **El Seibo:** Parque Nacional Los Haitises, entre la caseta #1, Cueva de Arena, y Boca de Infierno, 19°05′N, 69°27′30″W, *Zanoni et al. 35961* (NY). **Samaná:** Samaná Peninsula, Laguna, N of Pan de Azúcar, *Ekman 15099* (GH, US). **San Cristóbal:** near El Cacao, 500 m, *Liogier 17770* (F, NY). EL SALVADOR. **Santa Ana:** Finca Pilón on Cerro de los Naranjos, Volcán Santa Ana, *Williams et al. 15135* (F). GUATEMALA. **Alta Verapaz:** Cubilquitz, *von Tuerckheim 7920* (GH, NY, US). **Izabal:** Río Dulce between Livingston and 6 mi. upriver on N side, *Steyermark 39464* (A, F). **Petén:** La Cumbre, 5 km E on Pusila River bank, *Contreras 8873* (CAS, MO), *8893* (CAS, MO). **Quezaltenango:** Río Samala near Santa María de Jesús, *Standley 84616* (F). **San Marcos:** 6 mi. SW of Tajumulco, NW slopes of Volcán Tajumulco, *Steyermark 36731* (F, NY). **Sololá:** woods bordering Río Bravo in the vicinity of Finca Moca, S-facing slopes of Volcán Atitlán, *Steyermark 479564* (F, US). **Suchitepequez:** S-facing slopes of Volcán Santa Clara 1.5–2 mi. W of Finca El Naranjo, *Steyermark 46808* (F). HAITI. **Nord:** Massif du Nord, sobre Morne Bonnet Levèque, al SO de Milot, 19°6′N, 72°14′W, *Mejía 35780* (NY). HONDURAS. **Atlántida:** Lancetilla Valley near Tela, *Standley 52736* (A, F, US), *54583* (A, F, US), *55581* (A, F, US). **Cortes:** Santa Cruz de Yojoa, *Edwards 654* (A, US). **Santa Bárbara:** near Mochito, *Dickson 1352* (US). JAMAICA. **Cornwall:** Trelawney, Tyre near Troy, *Harris 9448* (F, NY, US). **Middlesex:** St. Catherine, Mt. Diablo, site of Blue Mountain, 2.5 mi. S by road of Hollymount Road, *Hespenheide et al. 1389* (DUKE, GH). **Surrey:** St. Thomas, trail from Bath to Corn Puss Gap, just S of the gap, *Anderson & Sternberg 3311* (DUKE, GH, US). MEXICO. **Chiapas:** mpio. Ocosingo, 5 km SW of Santo Domingo, 120 km SE of Palenque on road to Bonampak, *Davidse et al. 20416* (MO). **Oaxaca:** road between Ixtlán & Valle Nacional, 13 mi. by road above Valle Nacional, 17°40′N, 96°22′W, *Webster & Breckon 15378* (MO). **Tabasco:** mpio. Teapa, Puyacatengo, *Ventura 20644* (F, MO). **Veracruz:** municipio San Andrés Tuxtla, Los Tuxtlas biological station, 18°34′-36′N, 95°04–09′S, *Ibarra 202* (MO), *547* (NY), *1025* (NY), *1983* (MO), *1984* (MO), *Martínez 3075* (F, MO, US). NICARAGUA. **Matagalpa:** Los Tres Laureles, *Neill 7259* (MO). **Rivas:** Isla Ometepe, Volcán Concepción, Altagracia "La Sabana," 11°32′N, 85°35′W, *Robleto 138* (MO). **Zelaya:** Cerro Waylawas, 13°39′N, 84°48–49′W, *Stevens 7404* (MO).

10. Hillia maxonii Standley, J. Wash. Acad. Sci. 18: 163. 1928. TYPE: Nicaragua. Managua: Las Nubes and vicinity S of Managua, 800–900 m, 28 June 1928, *W. R. Maxon, A. D. Harvey & A. T. Valentine 7501* (holotype, US, photo F).

Cosmibuena rhizophorae Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 22: 178. 1940. TYPE: Colombia. Valle: Buenaventura Bay, 0 m, 13 Apr. 1939, *E. P. Killip 34972* (holotype, US, photo F; isotype, F).

Suffrutescent herbs or shrubs to 5(–15) m tall; bark gray-brown, smooth. Leaf blades elliptic to oblanceolate or suborbicular 2.5–10 cm long, 15–35 mm wide, obtuse to rounded at apex, cuneate to attenuate at base, coriaceous to usually thickly so; secondary veins pinnate, 4–5 pairs, plane, without domatia; margins flat; petioles 3–8(–15) mm long; stipules 12–32 mm long, 8–10 mm wide. Flowers solitary; peduncles 1–2(–4) mm long; bracts lacking or 1–3 × 1–2 mm; calyx limb lacking or divided to base, the lobes 4, 5–6 mm long, 0.5–2 mm wide, ligulate, acute; corollas salverform, white, the tube 42–55 mm long, the lobes 4, 15–27 mm long, 10–17 mm wide, elliptic, rounded; anthers 4, ca. 5 mm long, subsessile, with tips positioned ca. 3 mm below top of corolla tube; ovary 3–10 mm long; style ca. 15 mm long; stigmas ca. 7 mm long, linear, positioned below middle of corolla tube. Capsules 29–60 mm long including beak 1–3 mm long, 5–9 mm diam., not stipitate, smooth to slightly ridged longitudinally; seeds 2–4 × 0.5–1 mm, with filaments 6–13 mm long. Figure 13F, G.

Habitat, phenology, and distribution (Fig. 15). Central Nicaragua to Ecuador, in wet forests at 0–2400 m: montane regions, Nicaragua to Panama, to mangrove formations and along rivers, Panama to Ecuador. Collected in flower April, May, July to September, and December, in fruit January to March, May to July, November, and December.

This species is characterized by its coriaceous leaf blades that are obtuse to rounded at the apex and smooth to slightly ridged capsules. Plants from Colombia and Ecuador are apparently disjunct by several hundred miles from those of central Pan-

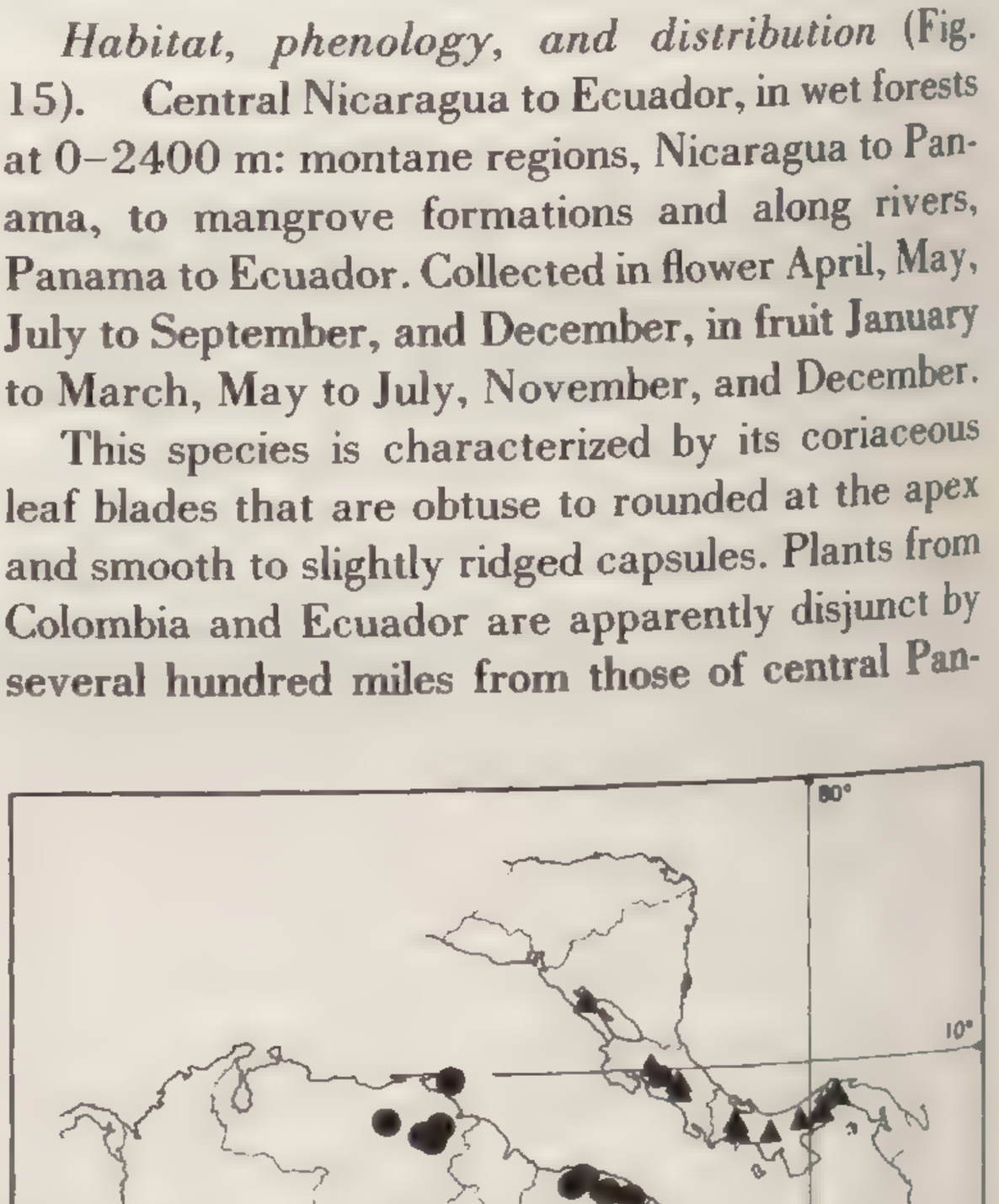

FIGURE 15. Distribution of *Hillia illustris* (Vell.) K. Schum. (solid circles) and *H. maxonii* Standl. (solid triangles) in Central and South America.

ama and are found in coastal formations rather than wet ridge forests. In Panama plants have been collected in both habitats. No morphological differences between the Central and South American plants are evident. *Cosmibuena macrocarpa* (Benth.) Walp. occupies a similar geographic range and set of habitats.

Hillia maxonii is similar to *H. tetrandra*, and these species have sometimes been combined (Dwyer, 1980). The distinctions between them are discussed under the treatment of the latter species. *Hillia maxonii* is also similar to *H. palmana* of southern Central America; this latter species has consistently smaller flowers and usually smaller leaves.

Representative specimens examined. COLOMBIA. **Chocó–Valle Border Region:** Alto del Galápago, along Ansermanuevo–San José del Palmar road, 4°40′N, 76°25′W, *Luteyn & Giraldo 12690* (CUVC). **Valle:** Estero del Cangrejal, entre los ríos Yurumanguí y Naya, *Cuatrecasas 16017* (F, US). COSTA RICA. **Alajuela:** La Palma de San Ramón, *Brenes 11900* (F, NY). **Cartago:** near La Sierra ca. 25 km S of Cartago, *Williams et al. 28129* (F). **Guanacaste:** El Silencio near Tilarán, *Standley & Valerio 44733* (US). **Heredia:** Cerros de Zurquí NE of San Isidro, *Standley & Valerio 50691* (US). **Puntarenas:** Monteverde Reserve, *Haber 571* (MO), *1787* (MO), *4501* (MO), *Hammel & Haber 13933* (MO). **San José:** near Finca La Cima above Los Lotes, N of El Copey, *Standley 42599* (US), *42771* (US). ECUADOR. **Carchí:** environs of Chical 12 km below Maldonado on Río San Juan, 1°04′N, 78°17′W, *Madison et al. 4700* (F). NICARAGUA. **Managua:** S of Managua, *Garnier 135* (F). PANAMA. **Bocas del Toro:** near Cerro Colorado ca. 9.4 mi. from Chami camp, 8°35′N, 81°45′W, *McPherson 8941* (MO). **Chiriqui:** distrito Boquete, Fortuna Dam site, *van der Werff & van Hardeveld 6722* (MO). **Coclé:** western slopes and summit of Cerro Valle Chiquito, *Seibert 495* (MO, US). **Panamá:** Cerro Jefe (Cerro Azul), 9°15′N, 79°23′W, *Dwyer & Gauger 7377* (GH, MO), *McPherson 6858* (MO), *7138* (MO), *Mori & Kallunki 6500* (MO, NY). **Veraguas:** 5 mi. W of Santa Fe on road past Escuela Agrícola Alto Piedras, *Croat 23079* (F, MO, NY).

11. Hillia palmana Standley, J. Wash. Acad. Sci. 18: 164. 1928. TYPE: Costa Rica. **Heredia: vicinity of La Palma on road to La Hondura 1500–1700 m, 17–18 July 1923, *W. R. Maxon & A. D. Harvey 8045*** (holotype, US).

Hillia chiapensis subsp. *grandifolia* Dwyer, Ann. Missouri Bot. Gard. 67: 216. 1980. TYPE: Panama. **Veraguas: 6–7 km W of Santa Fe on new road past** agriculture school, 2900 ft. [950 m], *M. Nee 9698* (holotype, MO).

Suffrutescent herbs or shrubs to 5 m tall; bark gray-brown, smooth. Leaf blades elliptic to oblanceolate, 2–7 cm long, 1.5–3.5 cm wide, obtuse to rounded or rarely truncate at apex, cuneate to attenuate at base, coriaceous; secondary veins pinnate, 3–4 pairs, plane, without domatia; margins flat; petioles 3–8 mm long; stipules 12–20 mm long, 8–10 mm wide. Flowers solitary; peduncles 1–2 mm long; bracts lacking or 1–3 × 1–2 mm; calyx limb lacking or divided to base, the lobes 4, 4–6 mm long, 1–2 mm wide, ligulate, acute to rounded; corollas salverform, white, the tube 35–40 mm long, the lobes 4, 8–12 mm long, 6–12 mm wide, elliptic to suborbicular, rounded; anthers 4, ca. 5 mm long, subsessile, with tips positioned 2–3 mm below top of corolla tube; ovary 3–5 mm long; style ca. 15 mm long; stigmas ca. 7 mm long, linear, positioned below middle of corolla tube. Capsules 3–6 cm long including beak 1–3 mm long, 5–8 mm diam., not stipitate, smooth; seeds 2–4 × 0.5–1 mm, with filaments 6–13 mm long. Figure 11D, E.

Habitat, phenology, and distribution (Fig. 16). Central Nicaragua to central Panama, in wet forests at 675–2500 m. Collected in flower December to October, most frequently May to June, in fruit December to February, May, and July to October.

This species is distinguished by its medium-sized leaf blades that are usually obtuse to rounded at the apex and small flowers. It is similar to *Hillia maxonii* and *H. panamensis*; the distinctions among these three species are discussed in the treatments of the last two species.

Representative specimens examined. COSTA RICA. **Alajuela:** Fila Volcán Viejo, San Carlos, *Gómez-Laurito 11095* (CR). **Cartago:** Volcán Irazú, SW slopes near Guayabillos, *Cufodontis 465* (F). **Guanacaste:** entre la laguna del Arenal y el Alto de La Carpintera, cerca de Tilarán, *Brenes 12644* (F, NY). **Heredia:** entre Finca La Georgina y Vara Blanca, *Jiménez 2075* (CR, F, NY). **Limón:** Reserva Indígena Talamanca, camino a Soki entre la quebrada Amubri, margen izquierda del río Lari, 9°29′40″N, 82°03′40″W, 200 m, *Chacón 18* (MO). **Puntarenas:** Monteverde area, 10°20′N, 84°50′W, *W. Haber 760* (MO), *1156* (MO), *4564* (MO), *6174* (MO), *Haber & Bello 3671* (CR, MO), *4263* (CAS, CR, MO), *4267* (CR, MO), *4530* (MO). **San José:** near Altos de Tablazo ca. 7 km SSE of Higuito, ca. 9 km SSE of Desemparados, *Wilbur 19782* (CAS, CR, F, MO, NY, US). NICARAGUA. **Boaco:** 2 km al N de San José de los Remates, 12°36′N, 85°45′W, *Moreno 24904* (MO), *24936* (MO). **Granada:** lado NO del volcán Mombacho, Finca San Joaquín, 11°50′N, 85°59′W, *Moreno & Henrick 8510* (MO). **Jinotega:** ca. 1.5 km from Hwy. 3 on road to Aranjuez, 13°02′N, 85°55′W, *Stevens 5947* (MO). **Matagalpa:** ridge along road between La Danta and La Luna, 12°40′N, 85°43′W, *Stevens 9616* (MO). PANAMA. **Bocas del Toro:** trail from Boquete to Cerro Pate Macho, 8°49′N, 82°24′W, *McPherson & Merello 8328* (MO). **Chiriquí:** vicinity of Fortuna Dam, 8°40′N, 79°50′W, *McPherson 10577* (MO). **Darién:** E slope of

FIGURE 16. Distribution of *Hillia palmana* Standl. (left-hand map) and *H. grayumii* C. M. Taylor (right-hand map) in Central America.

Cerro Sapo, *Hammel 1284* (MO). **Panamá:** E slope of Cerro Jefe (Cerro Azul), *Tyson 3436* (GH, MO). **Veraguas:** Cerro Tute, 8°32′N, 81°07′W, *Knapp & Dressler 5398* (MO), *Mori et al. 7559* (MO).

12. Hillia panamensis Standley, N. Amer. Fl. 32(2): 117. 1921. TYPE: Panama. Chiriquí: Cerro de la Horqueta around Los Siguas Camp, 1700 m, 17–19 Mar. 1911, *H. Pittier 3190* (holotype, US; isotype, US).

Hillia chiapensis Standl., J. Wash. Acad. Sci. 16: 16. 1926. TYPE: Mexico. Chiapas: near Fénix, Apr. 1925, *C. A. Purpus 262* (holotype, US, photo F).

Hillia hathewayi Fosberg, Sida 2: 387. 1966. TYPE: Costa Rica. Heredia: S slope of Volcán Barba, 1950 m, 26 May 1965, *W. H. Hatheway 1371* (holotype, US; isotypes, F, GH).

Suffrutescent herbs or shrubs to 4 m tall; bark gray-brown, smooth. Leaf blades elliptic to narrowly elliptic, 6–15 mm long, 3–10 mm wide, rounded to obtuse at apex, cuneate to attenuate at base, subcoriaceous to coriaceous; secondary veins pinnate, ca. 2 pairs, smooth, without domatia; margins flat; petioles 1–2 mm long; stipules 4–5 mm long, 1–1.5 mm wide. Flowers solitary; peduncles ca. 1 mm long; bracts lacking; calyx limb usually lacking or divided to base, the lobes 4, 6–7 mm long, 1–3 mm wide, ligulate, rounded; corollas white, salverform, the tube 24–35 mm long, the lobes 4, 8–10 mm long, 3–5 mm wide, lanceolate, acute; anthers 4, 1–2 mm long, subsessile, with tips positioned 1–2 mm below top of corolla tube; ovary 2–3 mm long; style 7–12 mm long; stigmas 5–10 mm long, linear, positioned below middle of corolla tube. Capsules 2–4 cm long including beak 1–2 mm long, ca. 3 mm diam., not stipitate, smooth or usually with ca. 10 longitudinal ridges; seeds 1–2 × 0.5 mm, with filaments 6–13 mm long. Figure 11F–I; Dwyer (1980: fig. 48, as *Hillia chiriquiensis*).

Habitat, phenology, and distribution (Fig. 12). Southern Mexico to Guatemala and Belize, and southern Nicaragua to western Panama, in wet forests at 20–2300 m. Collected in flower December, January, and June through August, in fruit November to April, August, and September.

This species is distinguished by its lanceolate acute corolla lobes and relatively small, usually narrow leaf blades, stipules, and capsules. The plants of southern Mexico and Guatemala are apparently disjunct from those of southern Central America, but no morphological differences are apparent and they appear to occupy similar habitats. Therefore *Hillia chiapensis* is here placed in synonymy. Similar apparently disjunct geographic ranges are seen in *H. loranthoides* and species of *Psychotria* (Hamilton, 1989).

Hillia panamensis is similar to *H. palmana*; the latter species has elliptic rounded corolla lobes 6–12 mm wide, and usually larger, proportionally broader leaf blades, stipules, and capsules.

Several sterile and fruiting specimens from relatively low elevations in Nicaragua and Costa Rica are provisionally included here, although they have relatively broad leaves and ridged capsules.

Representative specimens examined. BELIZE. **Toledo:** Maya Mountains, *Holst 4292* (MO). COSTA RICA. **Alajuela:** Cantón Alfaro Ruíz, Palmira, *Smith 2737* (F). **Cartago:** Turrialba, Instituto Interamericano de Ciencias Agrícolas, *León 2999* (CR). **Guanacaste:** El Dos de Tilarán, 13 km NW of Monteverde, 10°25′N, 84°55′W, 900 m, *Haber et al. 5273* (MO). **Limón:** Cerro Coronel, E of Laguna Danto, 10°41′N, 83°38′W, *Stevens 23919* (CR), *Stevens & Montiel 24389* (CR, MO). **Puntarenas:** Monteverde area, *Haber 384* (MO), *562* (MO). GUATEMALA. **Alta Verapaz:** between Finca Chimote near Rubeltien and Finca Cubilgüitz, *Steyermark 44195* (F, US). **Chiquimula:** Cerro Tixixí 3–5 mi. N of Jicotán, *Steyermark 31627* (F, NY). MEXICO. **Chiapas:** municipio de Ocosingo, near Laguna Ocotal Grande ca. 25–30 km SE of Monte Líbano, ca. 45 km E of Ocosingo, *Dressler 1487* (NY, US). NICARAGUA. **Rivas:** Isla de Ometepe, Volcán Maderas, 11°26–37′N, 85°30–33′W, *Moreno 18806* (MO), *19689* (MO), *19852* (MO), *Stevens 6552* (MO). PANAMA. **Bocas del Toro–Chiriquí Border:** Cerro Colorado, 8 km from intersection of the ridge road on the road to Escopeta, *Folsom 4785* (MO). **Panamá:** Cerro Jefe, *Hayden 1021* (MO).

4. Hillia subg. **Illustres** C. M. Taylor, subg. nov. TYPE: *Hillia illustris* (Vell.) K. Schum.

A subgeneribus ceteris *Hilliae* corollis infundibularibus 5–9-lobatis viridibus flavovirentibus vel colore atropureo suffusis et stigmatibus subcapitatis supra antheras positis differt.

Calyx limb lacking, very reduced, or with 5–9 well-developed lobes; *corollas* membranaceous to carnose, funnelform, green to yellow-green or flushed with dull dark purple, the lobes 5–9, triangular to suborbicular; *stamens* attached above middle or near top of corolla tube, the anthers

subsessile or with filaments well developed; *stigmas* subcapitate, positioned above anthers; *capsules* usually stipitate.

Seven species throughout northern and central South America, one extending north to Costa Rica.

13. Hillia grayumii C. M. Taylor, Selbyana 12: 137. 1991. TYPE: Costa Rica. Heredia: Finca La Selva, the OTS field station near Puerto Viejo de Sarapiquí, near the junction of the Ríos Puerto Viejo and Sarapiquí, 100 m, 5 May 1980, *M. H. Grayum 2793* (holotype, DUKE; isotype, DUKE).

Shrubs to 1 m tall, or lianas; bark gray-brown, smooth. Leaf blades elliptic, 9–16 cm long, 1.5–6.5 cm wide, acuminate at apex with tip 1–2 cm long, acute at base, coriaceous; secondary veins pinnate, 3–6 pairs, plane, without domatia; margins flat; petioles 3–20 mm long; stipules ca. 4 cm long, 6–8 mm wide. Flowers solitary; peduncles 2–3 mm long; bracts 1–2 mm long; pedicels 2–3(–5) mm long; calyx limb ca. 0.5 mm long, truncate to dentate; corolla broadly funnelform, bright pale green to yellow-green, the tube 43–50 mm long, the lobes 6, 8–9 mm long, triangular, obtuse to rounded; stamens 6, the filaments ca. 10 mm long, the anthers ca. 9 mm long, with tips positioned 3–5 mm below top of corolla tube; ovary 7–8 mm long; stigmas ca. 3 mm long, subcapitate, positioned immediately above anthers. Capsules ca. 12 cm long, ca. 12 mm diam., not stipitate, smooth or with 8–10 low longitudinal ridges; seeds ca. 3 × 0.5 mm, with filaments 15–16 mm long. Taylor et al. (1991: fig. 3).

Habitat, phenology, and distribution (Fig. 16). Costa Rica, in wet forest at 0–200 m. Collected in flower May and June, in fruit March.

This species is distinguished by its reduced calyx limb and bright pale green to yellow-green, broadly funnelform corollas. It is similar to *Hillia illustris* and *H. psammophila* of South America; the distinctions among these are discussed in the treatments of the other two species. Vegetatively *H. grayumii* resembles *H. triflora* var. *triflora*, with which it is sympatric, and these species can be difficult to separate in fruit.

Hillia grayumii appears to be uncommon and ephemeral. It was first discovered in a well-studied area of the La Selva Biological Station, where it apparently grew to flowering size rapidly, but within two years was no longer found in the vicinity (Hammel, pers. comm.; Grayum, pers. comm.).

Representative specimens examined. COSTA RICA. **Alajuela:** Monteverde Biological Reserve, Río Peñas Blancas, 10°19′N, 84°43′W, *Haber & Cruz 8464* (CR). **Cartago:** on Casa de Tajas ridge above Río Gato, 9°47′N, 83°41′W, *Lent 3703* (F, NY). **Limón:** shores of Caño Pereira, 10°45–47′N, 83°36–37′W, *Stevens et al. 25120* (CR, MO).

14. Hillia psammophila Steyermark, Mem. New York Bot. Gard. 19(5): 211. 1963. TYPE: Venezuela. Bolívar: vecinidad del Camp 125 en el Km 125, entre Luepa y Cerro Venamo, vecinidad de Cerro Uei, 1100 m, 20 Apr. 1960, *J. Steyermark & S. Nilsson 392* (holotype, VEN).

Suffrutescent vines, climbing by adventitious roots; bark smooth. Leaf blades elliptic to lance-elliptic, 4.5–6.5 cm long, 2–3 cm wide, acuminate at apex with tip 4–10 mm long, acute at base, coriaceous; secondary veins pinnate, 3–4 pairs, plane, without domatia; margins flat; petioles 6–11 mm long; stipules not seen. Flowers solitary; peduncles 4–5 mm long; bracts not seen; calyx limb divided to base, the lobes 6, ca. 18 mm long, 3–3.5 mm wide, triangular to narrowly elliptic, rounded; corollas funnelform, yellow-green, the tube ca. 6 cm long, the lobes 6, ca. 1 cm long, ca. 15 mm wide, rounded; anthers 6, sessile, 7–8 mm long, with tips positioned ca. 5 mm below top of corolla tube; ovary ca. 7 mm long; stigmas ca. 2 mm long, subcapitate, positioned immediately above anthers. Capsules not seen. Steyermark (1963: fig. 74).

Habitat, phenology, and distribution (Fig. 8). South-central Venezuela, in wet forests at 1100 m. Collected in flower in April.

This species is distinguished by its relatively small leaves and anthers situated just below the top of the corolla tube. The original and subsequent descriptions of this species (Steyermark, 1963, 1974) describe the filaments as ca. 15 mm long, but the anthers are sessile and the filaments adnate to the corolla for ca. 45 mm. *Hillia psammophila* is similar to *H. illustris*; the distinctions between them are discussed in the treatment of the latter species. *Hillia psammophila* is also similar to *H. grayumii* of Costa Rica and may be closely related; *H. grayumii* differs in its larger leaf blades, 9–16 cm long, and its anthers positioned just below the top of the corolla tube.

15. Hillia illustris (Vellozo) K. Schumann in Martius, Fl. Bras. 6(6): 202. 1889. *Saldanha illustris* Vell., Fl. Flum. 3: 141, t. 157. 1825. TYPE: Brazil. Rio de Janeiro area, Vell., Fl. Flum. t. 157, 1825, lectotype designated by Taylor (1993).

Hillia tubaeflora Cham., Linnaea 9: 260. 1834. TYPE:

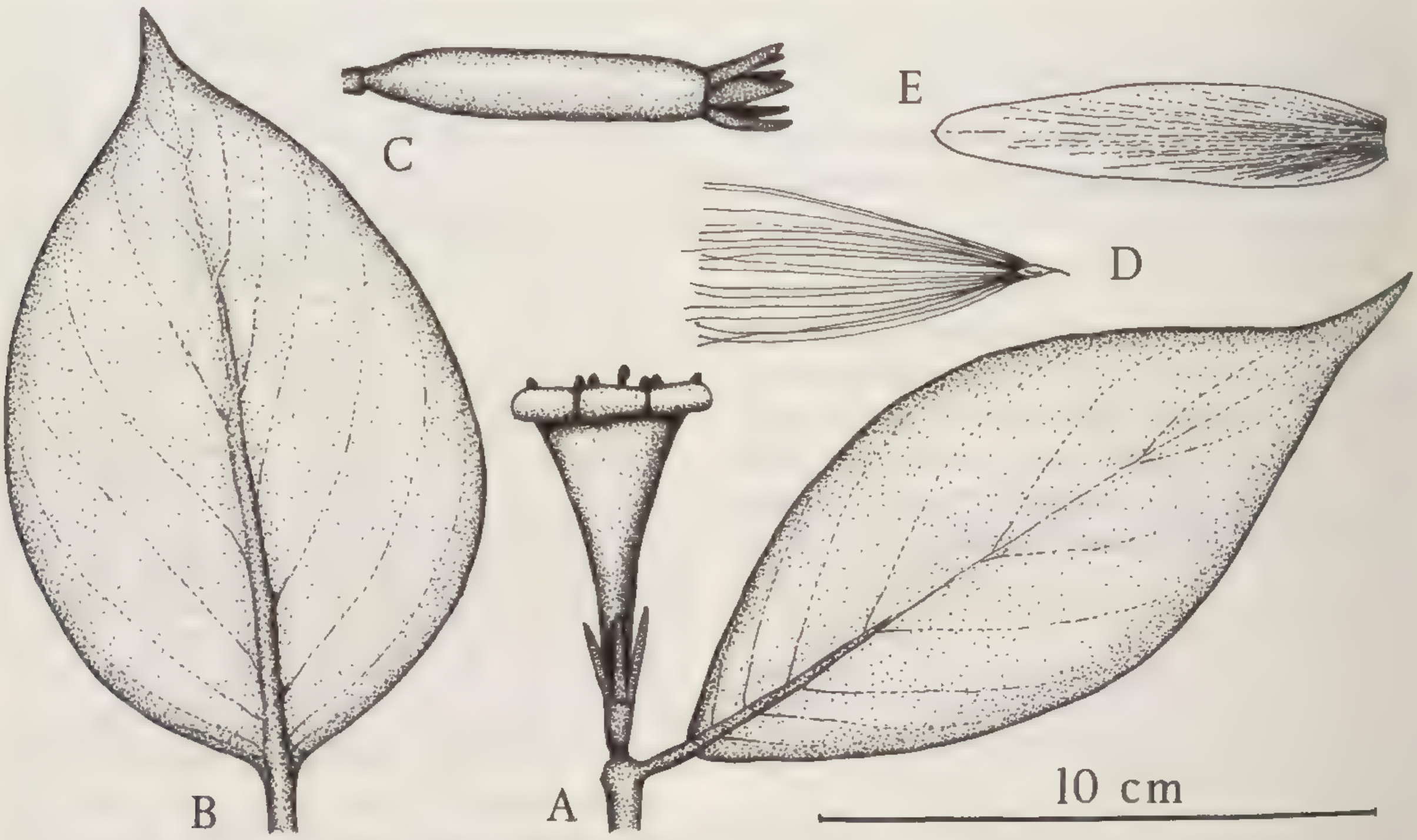

FIGURE 17. A–E. *Hillia illustris* (Vell.) K. Schum. —A. Habit with flower. —B. Leaf. —C. Capsule. —D. Seed. —E. Stipule (floral). A, E, from *Dusén 15539* (MO); B, from *Vásquez & Jaramillo 4130* (MO); C, D, from *Encarnación 26178* (MO). A–C to same scale, D to three times this scale, E to twice the first scale.

Brazil. Brazilia aequinoctialis, *Sello 5988* (holotype, B destroyed, photos F, GH, NY; isotype, F).

Hillia trinitensis R. O. Williams & Cheeseman, Fl. Trinidad & Tobago 2: 7. 1928. TYPE: Trinidad. Taruaria Forest, 16 Feb. 1915, *W. E. Broadway 7807* (lectotype, designated by Steyermark (1972: 288), NY; isotype, TRIN not seen).

Hillia goudotii Standl., Publ. Field Columbian Mus., Bot. Ser. 8: 338. 1931. TYPE: Colombia. Valle: Río Sucio, Jan. 1844, *J. Goudot s.n.* (holotype, P, photo F; isotype, F).

Suffrutescent herbs, shrubs, or small trees to 8 m tall; bark gray-brown to red-brown, smooth, sometimes peeling. Leaf blades elliptic, 8.5–15 cm long, 3–8 cm wide, acute to usually acuminate at apex with tip 5–10(–15) mm long, acute to cuneate at base, thickly coriaceous; secondary veins pinnate, 4–7 pairs, plane or with midrib sometimes prominulous abaxially, without domatia; margins flat; petioles 6–13 mm long; stipules subtending leaves 23–33 mm long, 7–10 mm wide, those subtending flowers 26–60 mm long, 6–18 mm wide. Flowers solitary(–3); peduncles 1–5 mm long; bracts not seen; calyx limb divided to base, the lobes 6, 9–35 mm long, often unequal by ca. 1 mm, 1.5–2(–4) mm wide, narrowly triangular, acute; corolla funnelform to broadly so, bright green to yellow-green, the tube 48–61 mm long, the lobes 6, 8–16 mm long, elliptic, obtuse to rounded; anthers 6, subsessile, 10–11 mm long, with tips positioned at or 1–2 mm above top of corolla tube; ovary 6–10 mm long with stipe 1–5 mm long; stigmas ca. 2 mm long, subcapitate, positioned immediately above anthers. Capsules with peduncles 2–10 mm long, (50–)85–115 mm long including beak 1–5 mm long, 8–15 mm diam., stipe 5–10 mm long, smooth or usually with ca. 10 low longitudinal ridges; seeds 2–4 × 0.5–2 mm, with filaments 14–22 mm long. Figure 17; Robbrecht (1988: fig. 6b, as *Hillia tubiflora*).

Habitat, phenology, and distribution (Fig. 15). Sporadic throughout tropical South America, in wet forests at 70–800 m, frequently along rivers. Collected in flower December, January, May to July, and September, in fruit January to March and May to November.

This species is distinguished by its relatively large, acute to acuminate leaf blades with pinnate venation and stipitate capsules. Both vegetative and reproductive parts vary rather widely in size, as in several other species of *Hillia*.

Hillia illustris is similar to *H. ulei*; the latter species is distinguished by its usually shorter, proportionally broader leaf blades with subpalmate venation. *Hillia illustris* also resembles *H. grayumii*, which has capsules that are not stipitate, a very reduced calyx limb, and filaments ca. 10 mm long, and *H. psammophila*, which has smaller leaf blades, filaments ca. 15 mm long, and anthers positioned below the top of the corolla tube.

There appears to be no morphological difference between plants of Trinidad and the mainland, and *Hillia trinitensis* is not maintained here. *Hillia goudotii*, based on a single specimen, differs from typical *H. illustris* only in having flowers borne in a cyme of three rather than solitary. A similar variation in flower number is seen in *H. saldanhae*, and the reverse variation, with flowers usually three but rarely one or two, is found in *H. triflora*. Therefore *Hillia goudotii* is not maintained here. Some authors (e.g., Robbrecht, 1988) have corrected the spelling of *H. tubaeflora* (tuba-shaped) to "tubiflora" (tube-shaped), but Chamisso based his description on a flowering specimen, and most likely intended to apply the first, more appropriate epithet.

Representative specimens examined. BOLIVIA. **Beni:** provincia Balliva, lower slopes of Serranía Pilón Lajas, 14.3 km N of bridge over Río Quiquibey, 15°19′S, 67°03′W, *Solomon 13957* (MO). **La Paz:** provincia Yungas Sur, basin of Río Bopi, Asunta near Evenay, *Krukoff 10697* (A, F, MO, NY). BRAZIL. **Amapa:** região de Río Jarí Monte Dourado, Planalto Amazônia, *Silva 927* (NY). **Paraná:** Tacarehy, *Dusén 15539* (F, GH, MO). **São Paulo:** Sete Varras, S entrance to Carlos Botelho State Park, 24°22′S, 46°55′W, *Gentry et al. 59053* (MO). COLOMBIA. **Amazonas–Vaupés Border:** río Apaporis, entre el río Pacoa y el rio Kanananari, Soratama, *Schultes & Cabrera 13030* (F, NY). **Chocó–El Valle Border Region:** carretera Ansermanuevo–San José de Palmar, Alto de Galápago, *Forero et al. 2868* (COL). **Vaupés:** Mitú and vicinity, island in Río Vaupés just below Urania, *Zarucchi et al. 1885* (COL, F, GH). ECUADOR. **Morona–Santiago:** Misión Bomboiza, 3°29′S, 78°34′W, *Holm-Nielsen & Jeppesen 4202* (AAU). **Napo:** cantón Tena, 10 km O de la estación biológica Jatún Sacha, carretera hacia Tena, 1°03′S, 77°40′W, *Palacios & Iguago 4433* (MO). FRENCH GUIANA. **Cayenne:** region de la Haute Armontabo (Bas Oyapock), *de Granville 4362* (COL, P). **Saint Laurent de Maroni:** Rivière Mana, Crique Arouany, *F. Hallé 622* (P). PERU. **Cuzco:** provincia La Convención, Camp Zero ca. 1 hour walk up Río Mapitunuari from Río Apurimac, Luisiana, *Dudley 11426* (F). **Huánuco:** provincia Leoncio Prado, distrito Rupa Rupa, al E de Tingo Maria, cerca al cerro Quemado, *Schunke 10292* (F, MO, NY). **Loreto:** provincia Maynas, distrito Alto Nanay, along trail to Santa Rosa, Santa María de Nanay, *Simpson & Schunke 806* (COL, F, MO, NY). SURINAM. **Brokopondo:** 2 km S of Affobakka along Sara Creek, Afterwards Lake, *van Donselaar 2109* (NY). **Marowijne:** ab Moengotapoe ad Grote Zwiebelswamp, *Lanjouw & Lindeman 628* (NY). **Nickerie:** Wilhelmina Gebegte, Zuid River 2 km above confluence with Lucie River, 3°10-20′N, 56°29 49′W, *Irwin et al. 55870* (COL, MO, NY). VENEZUELA. **Anzoátegui:** along Río León NE of Bergantín, *Steyermark 61433* (F). **Bolívar:** summit of W-facing escarpment E of Miamo, Hato de Nuria, Altiplanicie de Nuria, *Steyermark 88835* (NY). **Delta Amacuro:** departamento Antonio Díaz, Caño Guinquina, *Marcano et al. 70-2-77* (MO).

16. **Hillia ulei** K. Krause, Verh. Bot. Vereins Prov. Brandenburg 50: 97. 1908; K. Schum. ex Ule, in H. Karst. & Schenck, Vegetationsbilder 2, sub tab. 1–2: 3. 1904, nom. nud. TYPE: Peru. Loreto: prope Yurimaguas, Aug. 1902, *E. Ule 6305* (holotype, B destroyed, photos F, GH, MO, NY; isotype, F). Steyermark (1972) cited *Ule 6303* as the type collection, but this seems to be an error.

Hillia viridiflora Kuhlm. & Silveira, Arch. Jard. Bot. Rio de Janeiro 4: 370, t. 34. 1925. TYPE: Brazil. Rio de Janeiro: Rio de Janeiro Botanical Garden, Apr. 1920, *Ule RB-15737* (holotype, RB not seen; isotype, B destroyed, photos F, MO, NY, US).

Hillia irwinii Steyerm., Mem. New York Bot. Gard. 23: 287. 1972. TYPE: Brazil. Amapá: Río Jarí near Cachoeira Macacoara, 0°53′N, 53°21′W, 200 m, 26 Aug. 1961, *H. S. Irwin & W. A. Egler 46683* (holotype, NY; isotypes, F, GH, NY, US).

Hillia schultesii Steyerm., Mem. New York Bot. Gard. 23: 287. 1972. TYPE: Colombia. Amazonas–Vaupés border: río Apaporis, entre el río Pacoa y el río Kananari, boca del Pacoa, 250 m, 18 July 1951, *R. E. Schultes & Cabrera 13075* (holotype, US, photo NY).

Suffrutescent herbs or shrubs to 2 m tall; bark gray-brown, smooth. Leaf blades elliptic to broadly elliptic, 2–6.5(–7.5) cm long, 1.3–4 cm wide, acute to usually acuminate at apex with tip 3–5 mm long, rounded to cuneate at base, thickly coriaceous; secondary veins subpalmate, 5–7 pairs, plane or with midrib sometimes prominulous abaxially, without domatia; margins flat; petioles 4–11 mm long; stipules 5–17 mm long, 1.5–8 mm wide. Flowers solitary; peduncles 1.5–2 mm long; bracts lacking or 2–3 × 0.5–1.5 mm; calyx limb divided to base, the lobes 7–10, 8–15 mm long, often unequal by 1–3 mm, 1–2 mm wide, narrowly ligulate to triangular, acute to rounded; corollas broadly funnelform, bright green to yellow-green, the tube 28–39 mm long, lobes 7–10, 6–7 mm long, rounded; anthers 8, subsessile, 6–8 mm long, with tips positioned at top of corolla tube; ovary 5–10 mm long, stipes 8–10 mm long; stigmas ca. 2 mm long, subcapitate, positioned immediately above anthers. Capsules with peduncles 1.5–3 mm long, 6–10.2 cm long including beak 1–5 mm long, 8–10 mm diam., stipes 8–15 mm long, smooth; seeds 1–2 × 0.5–1 mm, with filaments 11–24 mm long. Figure 18.

Habitat, phenology, and distribution (Fig. 6). Sporadic throughout tropical South America and eastern Panama, in wet forests at 0–900 m, most frequently along rivers. Collected in flower March to May, July, and August, in fruit January, March to May, July to September, and November.

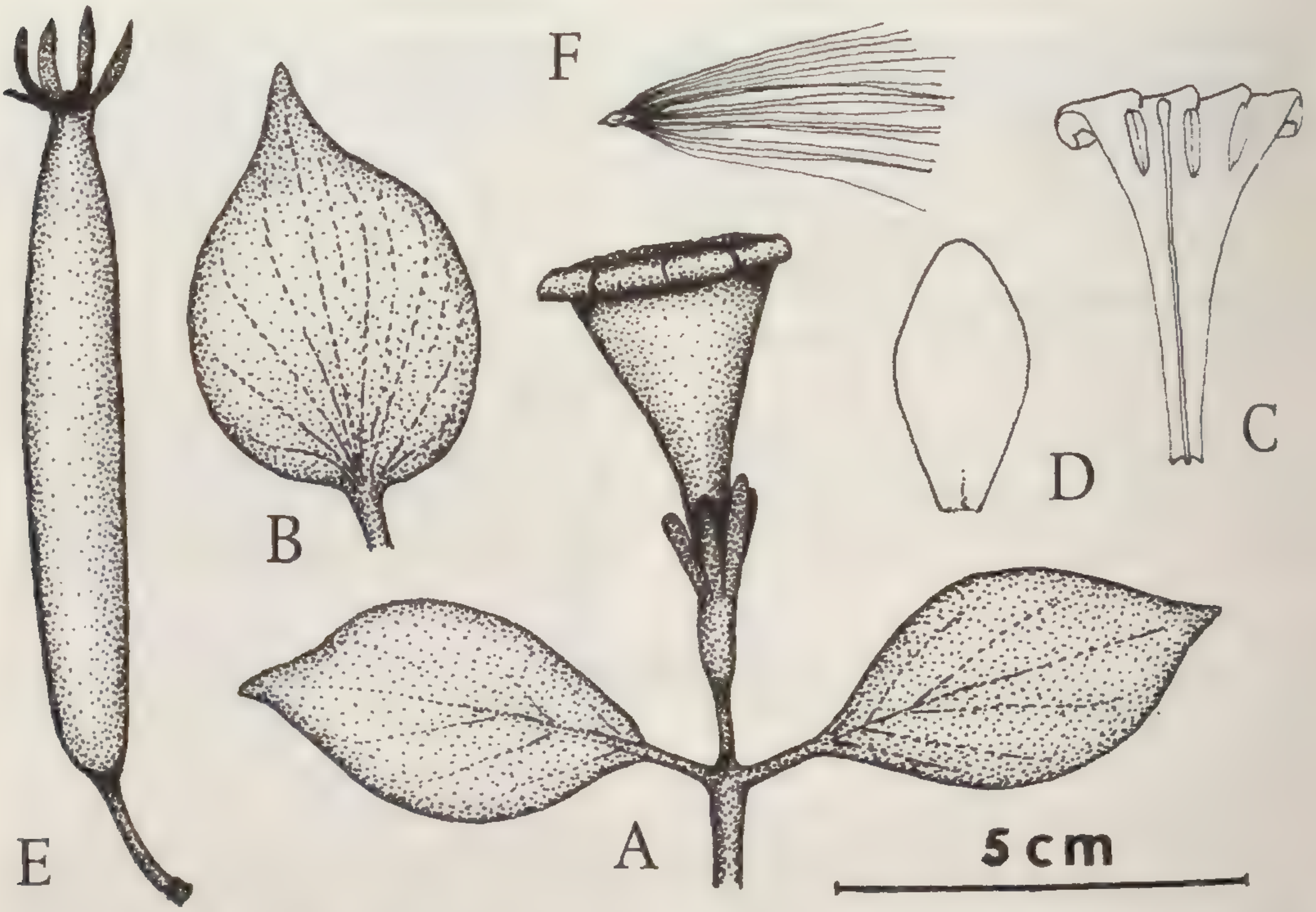

FIGURE 18. A–F. *Hillia ulei* K. Krause.—A. Habit with flower.—B. Leaf.—C. Flower opened.—D. Stipule (floral).—E. Capsule.—F. Seed. A, D, E, F, from *McDaniel & Rimachi 25763* (F); B, from *Schunke V. 4784* (F); D, from *Schultes 13075* (US). A–C, E to same scale; D, F to twice this scale.

This species is distinguished by its subpalmate leaf venation, otherwise in *Hillia* found only in *H. oaxacana* (subg. *Ravnia*) of Mexico. The green flowers usually become dark brown or black when dried. Size of both vegetative and reproductive structures varies, as does relative broadness of the leaf blades, stipules, calyx lobes, and corolla lobes. This variation is continuous, and shows no geographic pattern. Consequently several species recognized by Steyermark (1972) based only on wide geographic separation and differences in sizes of parts are not recognized here.

Steyermark separated *Hillia viridiflora* based on its corolla size, 3–3.5 cm long by 12 mm wide at the tube top in contrast to 4 cm long by 22 mm wide in *H. ulei*, and its "oblong-lanceolate" acute corolla lobes 5 mm wide, in contrast to lobes suborbicular, rounded, and 7 mm wide in *H. ulei*. Based on these criteria, *H. viridiflora* is represented by a single collection. However, collections included by Steyermark in *H. ulei* encompass the measurements of *H. viridiflora* in their range of corolla size and shape; additionally, the one flower available to characterize *H. viridiflora* appears to be immature, and thus probably not fully expanded in either the tube or the throat. The geographic disjunction between the type locality for *H. ulei* and the general range of this species further north no doubt influenced Steyermark's taxonomy. However, Ule brought many living collections from the Amazon basin to propagate in the Rio de Janeiro Botanical Garden, and Kuhlmann and Silveira stated in their species description that the plant appeared rather mysteriously, flowered, and disappeared from the Botanical Garden and was not seen elsewhere.

Steyermark separated *Hillia irwinii* based on its ten calyx lobes and corollas ca. 5 cm long with emarginate lobes, in contrast to calyx lobes five to eight and corollas 3–4.5 cm long with triangular lobes in his circumscription of *H. ulei*. Based on these criteria, *H. irwinii* is represented by two collections. However, by my measurement the corolla of the type collection is 43 mm long, and the corolla lobes of this specimen are rounded rather than emarginate. The type collection of *H. irwinii* has ten calyx and corolla lobes and the paratype collection has nine, in contrast to seven to eight calyx and corolla lobes in other specimens of *H. ulei*. However, calyx and corolla lobe number vary

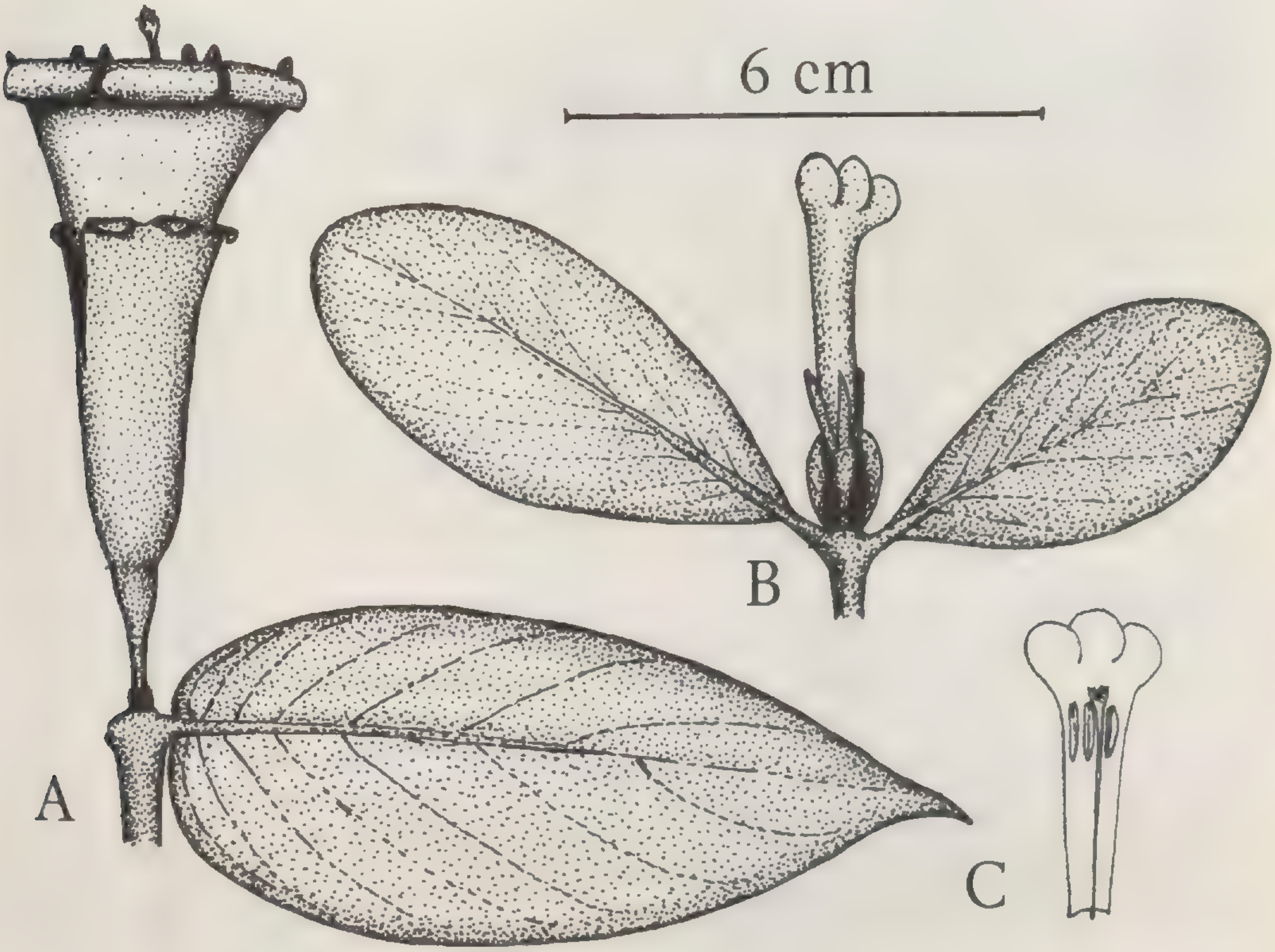

FIGURE 19. A. *Hillia costanensis* Steyerm.—A. Habit with flower. B, C. *Hillia saldanhae* K. Schum.—B. Habit with flower.—C. Flower opened. A, from *Bunting 14483* (NY); B, C, from *Glaziou 12790* (F). All to same scale.

in most species of *Hillia*, and the difference in number seen here alone does not seem to warrant separation of these species.

Steyermark separated *H. schultesii* based on its larger leaf blades, 8–11.5 cm long in contrast to 3.5–7 cm long in *H. ulei*, and its "acutish" calyx lobes in contrast to "rounded or obtuse" in *H. ulei*. Based on these distinctions, *H. schultesii* is represented by one collection. Its leaf blades are relatively long, but the "acutish" shape of its calyx lobes is very difficult to separate from the characteristically obtusely angled lobes of *H. ulei*. Given the relatively small number of collections of *H. ulei* available compared to its apparently large geographic range, separation of *H. schultesii* based only on these features seems unjustified.

Representative specimens examined. BOLIVIA. **La Paz:** provincia Yungas Sur, basin of Río Bopi, San Bartolomé near Calisaya, *Krukoff 10171* (A, F, MO). BRAZIL. **Acre:** Cruzeiro do Sul, Rio Jurua and Rio Moa, Estrada Alemanha, *Maas P12811* (NY). ECUADOR. **Napo:** Río Lagarto Cocha, near Redondo Cocha, 0°35'S, 75°15'W, *Lawesson et al. 44421* (AAU). PANAMA. **Darién:** Sumacate along Tuyra River, *Pittier 6594* (US). PERU. **Loreto:** Mishuyacu near Iquitos, *Klug 1182* (F, NY, US). **Madre de Dios:** Parque Nacional de Manú, Rio Manú, Cocha Cashu Station, 11°50'S, 71°25'W, *Foster 9667* (MO, NY). **San Martin:** provincia Mariscal Cáceres, distrito Tocache Nuevo, quebrada de Almendras, margen derecha del río Huallaga, *Schunke 4458* (COL, F, GH, MO, NY, US). SURINAM. **Nickerie:** lower slopes of Frederik Top, 3 km S of Juliana Top, Wilhelmina Gebergte, 3°36 41'N, 56°30 34'W, *Irwin et al. 54944* (F).

17. Hillia saldanhae K. Schumann in Mart., Fl. Bras. 6(6): 201. 1889. TYPE: **Brazil. Rio de Janeiro: Nova Friburgo, *A. Glaziou 12790*** (holotype, B destroyed, photos F, GH, MO, NY; isotypes, F, P not seen).

Shrubs; bark red-brown, smooth. Leaf blades elliptic to oblanceolate, 3–6.6 cm long, 1.4–3.2 cm wide, obtuse to rounded at apex, cuneate to acute at base, subcoriaceous; secondary veins pinnate, 7–8 pairs, plane, without domatia; margins flat; petioles 2–7(–10) mm long; stipules 12–15 mm long, 8–10 mm wide. Flowers solitary(–3); peduncles 1–2 mm long; bracts not seen; pedicels

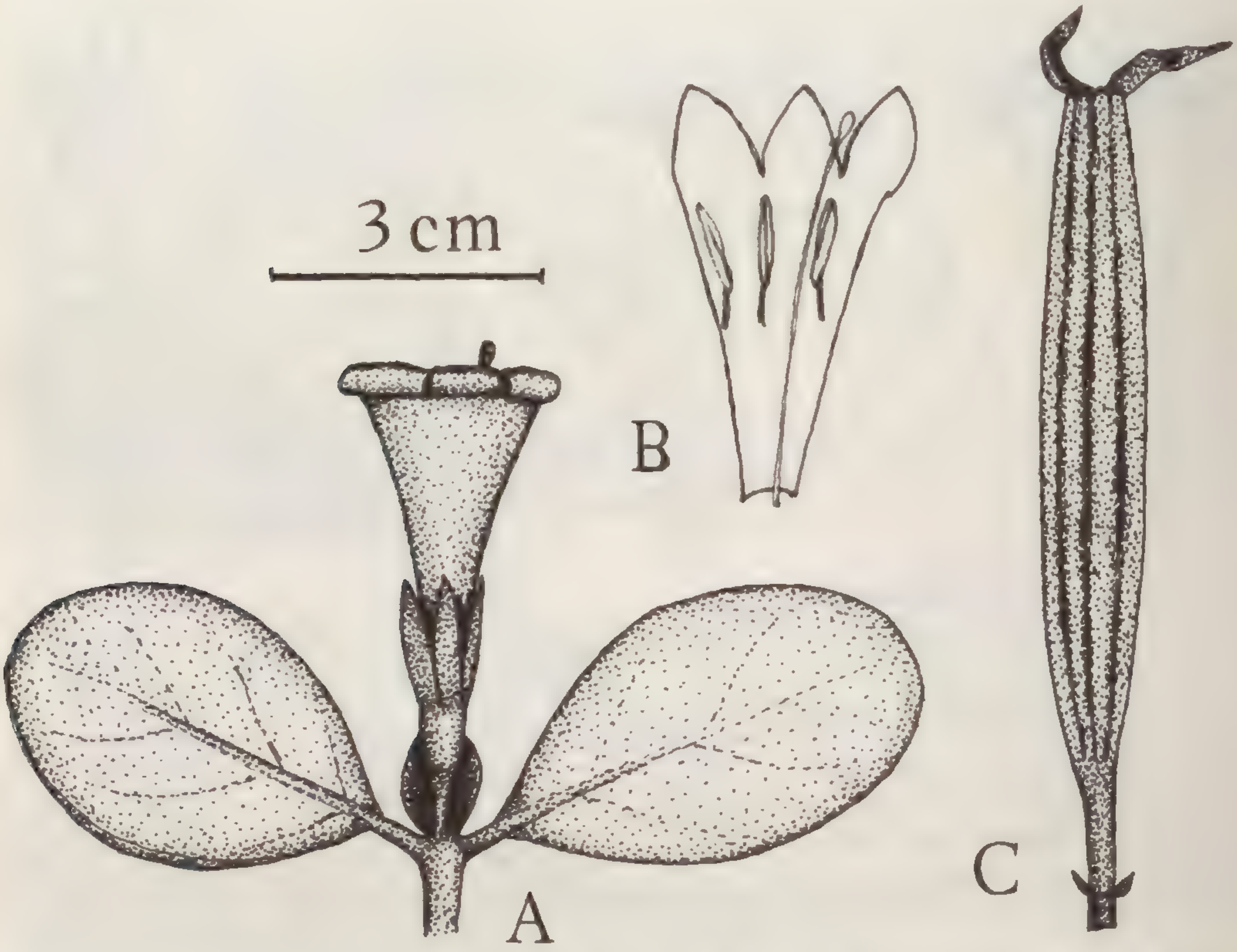

FIGURE 20. A–C. *Hillia foldatsii* Steyerm. —A. Habit with flower. —B. Flower opened. —C. Capsule. A, B, C, from *Holst 3772* (MO). All to same scale.

5–10 mm long; calyx limb divided to base, the lobes 5, 9–14 mm long, triangular, acute; corollas narrowly funnelform, the tube 30–35 mm long, the lobes 5, 5–7 mm long, suborbicular, rounded; anthers 5, subsessile, ca. 7 mm long, with tips positioned ca. 6 mm below top of corolla tube; ovary 2–5 mm long; stigmas 1.5–2 mm long, subcapitate, positioned immediately above anthers. Capsules ca. 25 cm long including beak 1–5 mm long, ca. 6 mm diam., not stipitate, smooth or with ca. 8 longitudinal ridges; seeds with filaments ca. 1 cm long. Figure 19A–C.

Habitat, phenology, and distribution (Fig. 6). Southeastern Brazil, in wet forest at ca. 100 m. Collection month unknown.

This name has been placed in synonymy with *Hillia parasitica*, but *H. saldanhae* clearly differs from *H. parasitica* in its rounded rather than acuminate leaf blades, five-lobed corollas and calyces, funnelform corollas with short lobes, and anthers positioned near the middle of the corolla tube. It differs from other species of subgenus *Illustres* by five-merous rather than six- to nine-merous corollas and anthers positioned near the middle rather than the top of the corolla tube. *Hillia saldanhae* resembles *H. foldatsii*; the distinctions between them are discussed in the treatment of the latter species. The corollas of the type collection, measured here, appear to be immature.

18. Hillia foldatsii Steyermark, Mem. New York Bot. Gard. 23: 290. 1972. TYPE: Venezuela. Bolívar: distrito Piar, Auyantepuí, Valle Orquídeas, parte noroeste, alrededores caída de agua Salto Angel, 1200 m, 17 Aug. 1968, *E. Foldats 7192* (holotype, VEN).

Shrubs ca. 1 m tall; bark red-brown, smooth. Leaf blades elliptic, 3–6.4 cm long, 1.5–3.5 cm wide, obtuse to rounded at apex, cuneate to rounded at base, thickly coriaceous; secondary veins pinnate, 2–5 pairs, plane or sometimes with midrib prominulous abaxially, without domatia; margins flat; petioles 3–6 mm long; stipules 9–12 mm long, ca. 8 mm wide. Flowers solitary, with peduncles 4–9 mm long; bracts 2–4.5 × 1–2.5 mm; calyx

limb divided to base, the lobes 6, 13–17 mm long, 3–6 mm wide, narrowly elliptic to ligulate, acute; corollas funnelform, green flushed with pink, the tube 35–60 mm long, the lobes 6, 7–9 mm long, suborbicular, rounded; stamens 6, the filaments 3 mm long, the anthers 9–10.5 mm long, with tips positioned ca. 3 mm below top of corolla tube; ovary 5–10 mm long with stipe 2–3 mm long; stigmas ca. 1 mm long, subcapitate, positioned 4–5 mm above top of corolla tube. Capsules 65–92 mm long including beak 1–5 mm long, 9–12 mm diam., the stipes 10–14 mm long, smooth or with ca. 10 low longitudinal ridges; seeds 2.5–3 × ca. 1 mm, with filaments ca. 12 mm long. Figure 20.

Habitat, phenology, and distribution (Fig. 8). Auyantepuí in southeastern Venezula on rocks in wet forest at 1200–1800 m. Collected in flower and fruit in March and August.

This species is distinguished by its thickly coriaceous leaf blades, six-merous flowers, and exserted stigmas. It is similar to *H. saldanhae*, with subcoriaceous leaf blades, smaller five-merous flowers, and included stigmas. Steyermark reported in the original description that the filaments are 15 mm long, but this has not been seen.

Additional specimens examined. VENEZUELA. **Bolívar:** distrito Piar, summit of Auyantepuí, 5°51′N, 62°32′W, *Holst 3772* (MO).

19. Hillia costanensis Steyermark, Mem. New York Bot. Gard. 23: 293. 1972. TYPE: Venezuela. Falcón: Sierra de San Luis, cerca del puente de Jobo, entre Curimagua y San Luis, 800–900 m, 20 July 1967, *J. A. Steyermark 99274* (holotype, VEN; isotypes, NY, P).

Hillia zuliaensis Steyerm., Ann. Missouri Bot. Gard. 71: 1176. 1985. TYPE: Venezuela. Zulia: distrito Mara, vicinity of Río Guasare between Rancho 505 and Cerro Yolanda, 10°53–56′N, 72°26–28′W, 200–270 m, 29 May 1980, *J. A. Steyermark 122876* (holotype, MO).

Suffrutescent herbs or shrubs to ca. 1 m tall; bark gray-brown, smooth. Leaf blades elliptic-oblong to ovate-oblong, 6–13 cm long, 2.3–6.5 cm wide, acute to usually acuminate at apex with tip 5–10(–15) mm long, rounded to slightly cordate at base, coriaceous; secondary veins pinnate, 4–8 pairs, plane or with midrib sometimes prominulous abaxially, without domatia; margins flat; petioles 1.5–3 mm long; stipules ca. 15 mm long, ca. 6 mm wide. Flowers solitary; peduncles 1–3 mm long; bracts lacking or ca. 1 mm long and wide; calyx limb with tube 33–56 mm long, sometimes splitting along one side, the lobes 6, 3–12 mm long, often unequal by 100%, obtuse; corollas funnelform, bright green to yellow-green, the tube 51–70 mm long, the lobes 6, 8–10 mm long, rounded; anthers 6, subsessile, 10.5–14 mm long, with tips positioned 1–3 mm above top of corolla tube; ovary 5–8 mm long with stipe 5–8 mm long; stigmas ca. 1.5 mm long, subcapitate, positioned immediately above anthers. Capsules 40–61 mm long including beak 1–5 mm long, 5–8 mm diam., stipes 4–8 mm long, smooth with ca. 10 longitudinal lines or low ridges; seeds ca. 3 × 1 mm, with filaments 8–10 mm long. Figure 19A; Steyermark (1974: fig. 23).

Habitat, phenology, and distribution (Fig. 8). North-central Venezuela to northeastern Colombia, in wet forests at 200–1300 m. Collected in flower March to May and July, in fruit March, June, and September.

This species is distinguished by its subsessile leaves with the blades rounded to slightly cordate at base and calyx limb with a well-developed tube. Both of these features are unique in *Hillia*. Steyermark distinguished *H. costanensis* and *H. zuliaensis* based on size differences of both vegetative and reproductive features and disjunct geographic ranges. However, with more material available the variation in size and the geographic range seems to be continuous.

Representative specimens examined. COLOMBIA. **Guajira:** serranía de la Macuira, cerro Kichuao, cerca del cerro Kalal, *Bernal & Sugden 85* (COL). **Magdalena:** municipio Santa Marta, Parque Nacional Natural Tayrona, cerro El Cielo, *Lorenzo & Barrera 3911* (COL). VENEZUELA. **Aragua:** distrito Girardot, Parque Nacional Henri Pittier, La Cumbre de Rancho Grande, 10°21′N, 67°39′W, *Davidse at al. 16723* (MO, NY). **Lara:** distrito Torres, Páramo Agua Linda, en la carretera Lara–Zulia ca. 35 km al E de El Venado, km 12–13, arriba de la aldea Palmarito, 10°10′N, 70°42′W, *Bunting & Fucci 13483* (NY). **Portuguesa:** 30 km W of Guanare by air along Río Tucupido, 9°02′N, 70°01′W, *Liesner et al. 12630* (MO). **Zulia:** Cerro Los Manantiales, E of Río Guasare, W of Hacienda Los Manantiales, 12 km W of Corpo Zulia Campamento Carichuano, 11°01′N, 72°20′W, *Steyermark et al. 123255* (MO).

5. Hillia subg. **Ravnia** (Oersted) C. M. Taylor, Selbyana 11: 30. 1989. *Ravnia* Oerst., Vidensk. Meddel. Dansk Naturhist. Foren. Kjoebenhavn 1852: 49. 1853. TYPE: *Ravnia triflora* Oerst. [= *Hillia triflora* (Oerst.) C. M. Taylor].

Five species, southern Mexico to Venezuela.

Taylor (1989) described this subgenus and later added two new species (Taylor, 1991), with no

change in its characterization except an expansion of the geographic range. The individual species are therefore not described or discussed here. The geographic range presented for *Hillia triflora* var. *triflora* by Taylor (1989) should be emended to exclude the record from southern Mexico; this was based on a misidentification of a fruiting specimen of *H. loranthoides*. Species placed in this subgenus are *H. allenii* Steyerm., *H. longifilamentosa* (Steyerm.) C. M. Taylor, *H. oaxacana* C. M. Taylor, *H. rivalis* C. M. Taylor, and *H. triflora* (Oerst.) C. M. Taylor.

Excluded Species

Hillia chiriquiensis Dwyer, Ann. Missouri Bot. Gard. 67: 216. 1980. = *Cosmibuena valerii* (Standl.) C. M. Taylor (Taylor, 1992).

Hillia liguliflora Dwyer, Ann. Missouri Bot. Gard. 67: 216. 1980. = *Cosmibuena valerii* (Standl.) C.M. Taylor (Taylor, 1992).

Hillia longiflora Blanco, Fl. Filip. 235. 1837, not *Hillia longiflora* Sw. = *Elytranthe ampullacea* (Roxb.) Engl. (Merrill, 1918).

Hillia longiflora Hort ex Lem., in Van Houtte, Fl. Serres 3(1): 188. 1847, not *Hillia longiflora* Sw. = *Fagraea zeylanica* Thunb., Loganiaceae.

Hillia prasiantha Lem., in Van Houtte, Fl. Serres 3(1): 188. 1847. = *Fagraea zeylanica* Thunb., Loganiaceae.

Hillia valerii Standl., J. Wash. Acad. Sci. 16: 164. 1928. = *Cosmibuena valerii* (Standl.) C. M. Taylor (Taylor, 1992).

Literature Cited

Andersson, L. & C. Persson. 1991. Circumscription of the tribe Cinchoneae (Rubiaceae) – A cladistic approach. Pl. Syst. Evol. 178: 65 -94.

Bentham, F. & J. D. Hooker. 1873. Rubiaceae. *In:* Genera Plantarum 2: 7 151. Lovell Reeve, London.

Borhidi, A. 1982. Studies in Rondeletieae (Rubiaceae), III. The genera *Rogiera* and *Arachnothryx*. Acta Bot. Acad. Sci. Hung. 28: 65–71.

Bremekamp, C. E. B. 1966. Remarks on the position, the delimitation, and the subdivision of the Rubiaceae. Acta Bot. Neerl. 15: 1 33.

Bremer, B. 1987. The sister group of the paleotropical tribe Argostemmateae: A redefined neotropical tribe Hamelieae (Rubiaceae, Rubioideae). Cladistics 3: 35–51.

——— & R. Jansen. 1990. Comparative restriction site mapping of chloroplast DNA implies new phylogenetic relationships within Rubiaceae. Amer. J. Bot. 78: 198–213.

Candolle, A. P. de. 1830. *Hillia*. Prodromus Systematis Naturalis Regni Vegetabilis 4: 350-351. Treuttel & Würtz, Paris.

Dwyer, J. D. 1980. Rubiaceae. *In:* R. E. Woodson, Jr. & R. W. Schery & Collaborators, Flora of Panama—Part IX. Ann. Missouri Bot. Gard. 67: 1-522.

Ewel, J. S. & J. Whitmore. 1972. Ecological life zones of Puerto Rico and the U.S. Virgin Islands. U.S. Dept. Agric., Forest Service Research Paper ITF-18.

Farris, J. S. 1988. Hennig86, Version 1.5, Program and User's Reference. State Univ. of New York, Stony Brook.

Hamilton, C. 1989. A revision of Mesoamerican *Psychotria* subg. *Psychotria* (Rubiaceae). Ann. Missouri Bot. Gard. 76: 76–111, 386–429, 886–916.

Howard, R. A. 1989. Rubiaceae. *In:* Flora of the Lesser Antilles: Leeward and Windward Islands 6: 389-470. Arnold Arboretum, Harvard University, Jamaica Plain, Massachusetts.

Kirkbride., J. H., Jr. 1968. A revision of the Panamanian species of *Rondeletia*. Ann. Missouri Bot. Gard. 55: 372–391.

Kirkbride, M. C. G. 1982. A preliminary phylogeny for the neotropical Rubiaceae. Pl. Syst. Evol. 141: 115–122.

Lamarck, J. L. M. 1792. Tableau Encyclopédique et Méthodique. Botanique. Chez Pancoucke, Paris.

Lorence, D. 1991. New species and combinations in Mexican and Central American *Rondeletia* (Rubiaceae). Novon 1: 135–157.

Mena, P. 1990. A revision of the genus *Arcytophyllum* (Rubiaceae: Hedyotideae). Mem. New York Bot. Gard. 60: 1–26.

Merrill, E. D. 1918. Species blancoanae. Dept. Agric. & Nat. Resources, Bureau of Sci. Publ. #12, Manila.

Moore, S. le M. & A. B. Rendle. 1936. Rubiaceae. *In:* W. Fawcett & A. B. Rendle (editors), Flora of Jamaica 7: 1–132. British Museum (Natural History), London.

Robbrecht, E. 1988. Tropical woody Rubiaceae. Opera Bot. Belg. 1: 1–271.

Roemer, J. J. 1796. Scriptores de Plantis Hispanicis, Lusitanicis, Brasiliensibus. Raspeana, Nuremburg.

Sastre, C. & J. Portecop. 1985. Plantes Fabuleuses des Antilles. Editions Caribéenes, Paris.

Schumann, K. 1889. *Hillia*. *In:* C. Martius, Flora Brasiliensis 6(6): 200–203.

———. 1891. Rubiaceae. *In:* A. Engler & K. Prantl (editors), Die Natürlichen Pflanzenfamilien 4: 1–156. Wilhelm Engelmann, Leipzig.

Sims, J. 1804. *Hillia longiflora*. Bot. Mag. 19: fig. 721.

Smith, J. E. 1814. An Introduction to Physiological and Systematical Botany. Bradford & Read, Boston.

Standley, P. C. & L. O. Williams. 1975. Flora of Guatemala -Part IX (Rubiaceae). Fieldiana, Bot. 24(9): 1–274.

Steyermark, J. A. 1963. *Hillia*. *In:* B. Maguire & Collaborators, The Botany of the Guayana Highland. Part V. Mem. New York Bot. Gard. 10: 209 212.

———. 1967. *Rondeletia, Arachnothrix*. *In:* B. Maguire & Collaborators, The Botany of the Guayana Highland. Part VII. Mem. New York Bot. Gard. 17: 241–261.

———. 1972. *Hillia*. *In:* B. Maguire & Collaborators, The Botany of the Guayana Highland. Part IX. Mem. New York Bot. Gard. 23: 285-295.

———. 1974. Rubiaceae. *In:* T. Lasser (editor), Flora de Venezuela 9: 1–2070. Ministerio de Agricultura y Cría, Dirección de Recursos Naturales Renovables, Instituto Botánico, Caracas.

Swartz, O. 1791. Observationes Botanicae. J. J. Palm, Erlangen.

SWOFFORD, D. 1990. PAUP—Phylogenetic Analysis Using Parsimony, Version 3.0, Program and User's Guide. Illinois Nat. Hist. Survey, Urbana.

TAYLOR, C. M. 1989. Revision of *Hillia* subg. *Ravnia* (Rubiaceae: Cinchonoideae). Selbyana 11: 26–34.

———. 1991. Two new species of *Hillia* subg. *Ravnia* (Rubiaceae) from Venezuela and Mexico. Ann. Missouri Bot. Gard. 78: 521–523.

———. 1992. Revision of *Cosmibuena* (Rubiaceae). Ann. Missouri Bot. Gard. 79: 886–900.

———. 1993. *Hillia*. *In:* G. Harling & L. Andersson, Flora of Ecuador 50: 93–102. Distributed by the Council for Nordic Publications in Botany, Gothersgade 130, DK-1353, Copenhagen.

VERDCOURT, B. 1958. Remarks on the classification of the Rubiaceae. Bull. Jard. Bot. État 28: 209–290.

———. 1988. *Hymenodictyon*. Pp. 452–455 *in* D. Bridson & B. Verdcourt, Flora of Tropical East Africa. Rubiaceae (Part 2). A. A. Balkema, Rotterdam.

NUMERICAL LIST OF SPECIES OF *HILLIA*

1. *Hillia* subg. *Hillia*
   1. *H. wurdackii* Steyerm.
   2. *H. macrophylla* Standl.
   3. *H. macromeris* Standl.
   4. *H. bonoi* Steyerm.
   5. *H. killipii* Standl.
   6. *H. parasitica* Jacq.
2. *Hillia* subg. *Andinae* C. M. Taylor
   7. *H. macbridei* Standl.
3. *Hillia* subg. *Tetrandrae* C. M. Taylor
   8. *H. loranthoides* Standl.
   9. *H. tetrandra* Sw.
   10. *H. maxonii* Standl.
   11. *H. palmana* Standl.
   12. *H. panamensis* Standl.
4. *Hillia* subg. *Illustres* C. M. Taylor
   13. *H. grayumii* C. M. Taylor
   14. *H. psammophila* Steyerm.
   15. *H. illustris* (Vell.) K. Schum.
   16. *H. ulei* K. Krause
   17. *H. saldanhae* Schum.
   18. *H. foldatsii* Steyerm.
   19. *H. costanensis* Steyerm.
5. *Hillia* subg. *Ravnia* (Oerst.) C. M. Taylor
   20. *H. oaxacana* C. M. Taylor
   21. *H. allenii* Steyerm.
   22. *H. longifilamentosa* (Steyerm.) C. M. Taylor
   23. *H. rivalis* C. M. Taylor
   24a. *H. triflora* Oerst. var. *triflora*
   24b. *H. triflora* var. *pittieri* (Standl.) C. M. Taylor

NUMBERED COLLECTIONS OF *HILLIA* EXAMINED

Specimens are listed alphabetically by principal collector. Identifications are indicated by the numbers in parentheses following the collection number. The numbers in parentheses correspond to the numbers designating the species in the text. Asterisks indicate type collections. All collections cited in the text are included here, along with additional collections of all species not cited in the text.

Abbott, W. L. 365 (9); 2357 (6). Acevedo, P. 2990 (6). Ackerman, J. D. 1537 (6). Adams, C. D. 11717 (9). Alain, Bro. 3856 (9); 6034 (9). Allen, P. H. 1872 (10); 3682 (10). Alvarez, H. J. 24 (6). Anderson, W. R. 3311 (9); 35844 (6); 35914 (6). Antonio, T. 5078 (10). Aristeguieta 4239 (6). Arnoldo, Fr. M. 3302 (6). Asanza, E. 41098 (15); 41192 (15). Asplund, E. 10160 (2); 19403 (2); 19458 (3); 19481 (5). Axelrod, F. 240 (6).

Barbosa, C. 1906 (6). Barbour, P. 2614 (6). Beaman, J. H. 5185 (9); 6071 (9); 6105 (9); 6475 (9). Belanger 132 (6); 395 (6); 540 (6). Bello, E. 844 (8). Bena, P. 460 (6); 461 (6); 1110 (6); 1163 (6); 1225 (6). Benavides, O. de 9602 (2). Benítez de Rojas, C. D. 1069 (19). Berlin, B. 429 (3). Bernal, H. 48 (19); 85 (19). Berry, P. 3468 (6). Billiet, F. 1916 (15). Blackmore, S. 4104 (9). Blomquist, H. L. 13217 (6). Boldingh, I. 2198B (6). Boom, B. M. 1141 (6); 6901 (6); 6933 (6). Bono, J. 3797 (4). Boudet Fernandes, H. Q. 1830 (6); 2280 (6). Brade, A. C. 6830 (6). Brandebyge, J. 30601 (15); 33903 (15); 33962 (16); 42671 (15). Bresolin, A. 808 (6); 1037 (6). Breedlove, D. E. 31213 (8); 35025 (9); 35244 (9); 48354 (9); 49178 (9); 53555 (12); 56648 (12); 57488 (8); 68610 (8). Brenes, A. 3839 (8); 3847 (8); 3900 (8); 4852 (8); 5439 (8); 6137 (8); 11900 (10); 12644 (11); 15653 (11); 18919 (8). Britton 219 (6); 557 (9); 697 (6); 741 (9); 924 (6); 2020 (6); 2203 (6); 2591 (6); 3377 (6); 3511 (9); 5525 (6); 6378 (6); 5007 (9); 6541 (6); 7561 (6). Broadway, W. E. 5709 (6); 7807* (15). Brooke, W. M. A. 6700 (6). Bucher, G. C. 47 (9). Buchtien, O. 2217 (6); 5636 (6). Bunting, G. S. 13483 (19). Burch, D. 1371 (6). Byer, M. D. 66-383 (6).

Calzada, J. I. 604 (9). Camp, W. H. E2405 (5). Cárdenas 5995 (6). Cardona, F. 207 (6). Carrasquillo 40 (6). Cedillo T., R. 1887 (9); 2757 (9). Chacón, A. 18 (11). Chazaro B., M. 448 (9); 3380 (9). Christ 2188 (6). Churchill, H. W. 5521 (11). Clemente, Bro. 2321 (9); 6626 (9); 7144 (9). Contreras, E. 3024 (9); 5370 (9); 6959 (9); 7911 (9); 8873 (9); 8893 (9). Core, E. L. 1327 (6). Cosentino, K. 21 (9). Correa, M. D. 941 (10); 1770 (12); 2559 (11). Crankshaw, W. 4 (9). Croat, T. B. 14801 (10); 20709 (15); 21093 (6); 23079 (10); 26957 (12); 60971 (6); 63462 (8). Cuatrecasas, J. 12398 (2); 16017 (10); 19988 (10); 23963 (2). Cufodontis, G. 465 (11).

D'Arcy, W. G. 1812 (6). Davidse, G. 16723 (19); 20416 (9); 20716 (6); 24028 (11); 25503 (11). Dávila, E. N. 2 (6); 8 (6). de Jesús J., J. 3459 (6). Devia, W. 2572 (2). Díaz, C. 602 (16); 2491 (15). Díaz, S. 2302 (6); 4184 (6). Dickson, J. D. 1352 (9). Dodson, C. H. 1875 (6); 7783 (2); 9136 (2); 10195 (2); 10285 (6); 11852 (6). Donselaar, J. van 2109 (15). Dorantes, B. 3465 (9). Dressler, R. L. 1487 (12); 3522 (11). Drew, W. B. E-553 (2). Dryer, V. J. 1512 (11); 1597 (11). Duarte, A. P. 6257 (6); 11481 (6); 11570 (6). Dudley, T. R. 10414 (6); 11426 (15). Dusén, P. 8109 (6); 8689 (6); 8881 (6); 15538 (6); 15539 (15); 16113 (6). Duss, Père 342 (6); 1462 (6); 2546 (6). Dwyer, J. D. 7377 (10); 10022 (9); 10797 (9).

Edwards, J. B. 654 (9). Eggers, B. 6754* (6). Egler, W. A. 46683 (16). Ekman, E. L. 3775 (6); 4405 (6); 7867 (9); 9989 (9); 15099 (9). Encarnación, F. 26178 (15). Ernst, W. R. 1012 (6). Evans, L. 167 (6). Eyerdam, W. J. 393 (6).

Ferreyra, R. 1666 (6); 2255 (8). Folsom, J. P. 4785 (12); 9807 (11). Forero, E. 2868 (15). Fosberg, F. R. 51339 (6). Foster, R. 9667 (16).

Galarza, M. 110 (6). Galeano, G. 204 (2). Garnier, H. A. 135 (10). Gaudichaud 625 (6). Gentle, P. H. 3006 (9); 4847 (9); 4930 (9); 8939 (9). Gentry, A. 24168 (2); 35166 (2); 40719 (10); 45322 (6); 50447 (6); 50701 (6); 50959 (6); 50959A (9); 52091 (6); 59053 (15);

60342 (2); 60442 (2); 72567 (6); 77121 (9). Ginzberger, A. 273 (6). Glaziou, A. 6588 (6); 12790A (15); 13943 (6). Gómez G., L. D. 23593 (8). Gómez L., J. 11095 (11); 11302 (11). Gómez P., A. 4525 (9); 5447 (9). Gounelle 63 (6). Granville, J. J. de 4362 (15); 5856 (6); 6146 (15); 6215 (6); 6519 (15); 6797 (15); 8563 (6). Grayum, M. 2793 (13).

Haber, W. 384 (12); 562 (12); 571 (10); 760 (11); 1156 (11); 1342 (11); 1787 (8); 3671 (11); 3672 (12); 4263 (11); 4267 (11); 4501 (8); 4530 (11); 4564 (11); 5273 (12); 5275 (10); 6174 (11); 7000 (8); 7083 (11); 7334 (11); 8370 (8); 8393 (8); 8464 (13); 8914 (11). Hahn, L. 959 (6). Hallé, F. 591 (15); 622 (15); 698 (6). Hammel, B. E. 1284 (11); 2212 (11); 13930 (11); 13933 (10); 17336 (13). Hamilton, C. 4042 (10). Harley, R. M. 19309 (6); 19684 (6); 20860 (6); 27773 (6). Harling, G. 3884 (6); 11639 (6); 12475 (6); 24490 (3). Harris, W. 5465 (9); 9448 (9). Hartley, T. G. 13342 (6). Harvard Tropical Botany Course 797 (9). Hatheway, W. H. 1371* (11). Hatschbach, G. 7172 (6); 14528 (6); 18509 (6); 20831 (15); 23346 (6); 25789 (6); 28833 (6); 29669 (15); 39314 (6); 40653 (6); 43257 (6); 46043 (6). Hayden, Sr. M. V. 1021 (12). Heller, A. A. 4612 (6). Henrich, J. E. 406 (11). Hernández G., H. 124 (9); 1244 (9). Hernández M., R. 1256 (9); 1374 (9). Herrera Ch., G. 438 (10); 564 (8); 674 (11); 1320 (2); 3910 (10). Hespenheide, H. A. 519 (6); 541 (6); 986 (9); 1389 (9). Hioram, Bro. 4259 (9). Hodge, W. T. 702 (6); 1802 (6); 1663 (6); 1839 (6); 2587 (6); 3110 (6). Hoehne, F. C. 11504 (6). Holm-Nielsen, L. 4202 (15); 6124 (6). Holst, B. K. 3772 (18); 4292 (12). Hoover, W. S. 1920 (3). Howard, R. A. 10587 (6); 11515 (6); 11832 (6); 11954 (6); 12277 (6); 13436 (9); 14290 (9); 15540 (6); 16052 (6); 16053 (6); 16634 (6); 16889 (6); 17553 (6); 17675 (6); 19404 (6). Houghton, W. M. 1194 (6). Huber, O. 6316 (6); 8085 (6). Hunt, D. R. 6473 (6). Hutchison, P. C. 6799* (1).

Ibarra M., G. 202 (9); 547 (9); 1025 (9); 1983 (9); 1984 (9). Idrobo, J. M. 1059 (2); 2356 (6). Iltis, H. H. G202 (8). INBio-I 181 (11). Irwin, H. S. 19852 (6); 30209 (6); 54944 (16); 55298 (15); 55870 (15).

Jack, J. G. 6812 (9); 7211 (9); 8572 (9). Jacobs, B. 2265 (13). Jameson, W. 532 (6). Jaramillo A., J. L. 56 (5); 6897 (15). Jaramillo M., R. 7072 (6); 2748A (2). Játiva, C. 285 (2). Jean-Pierre, L. L. 238 (6). Jelski, C. de 367 (6). Jérémie, J. 832 (6); 1040 (6); 1099 (6); 1284 (6). Jiménez M., A. 2075 (11). Johnston, J. R. 41 (6); 1563 (6). Jorgensen, O. H. 40 (6). Jousson, J. 624A (6). Judd, W. S. 1508 (6).

Kennedy, H. 578 (11). Killip, E. P. 20685* (5); 34972* (10); 38670 (10). Kirkbride, J. H., Jr. 858 (10); 2398 (6). Klein, R. M. 7889 (6); 10641 (6); 10758 (6). Klug, G. 1182 (16); 3145 (5). Knapp, S. 2159 (10); 2621 (10); 4161 (11); 4205 (10); 4953 (11); 5398 (11); 7492 (1). Krukoff, B. A. 10171 (16); 10697 (15). Kuhlmann, G. G. 15737* (16). Kuhlmann, M. 1750 (6). Kuntze, O. 486 (6).

Landrum, L. R. 4273 (6). Lanjouw, J. 628 (15). Lankester, C. H. 1935 (11). Lanna 1922/1463 (6). Lawesson, J. E. 44288 (15); 44317 (15); 44421 (16). Lawrance, A. E. 351 (6). Lawton, R. O. 1254 (11). Lehman BT 416* (3). Lemos, C. 28681 (6). Lent, R. W. 1692 (8); 3703 (13). León, Bro. 6626 (9); 7854 (9); 19805 (9). León, J. 2999 (12). Lewis, M. 40471 (16). Liebmann 15419 (9). Liesner, R. 8170 (6); 8423 (6); 12360 (19); 12775 (6); 18431 (6). Lindeman, J. C. 13462 (6). Linden 786 (6); 2169 (6). Liogier, A. H. 11207 (6); 14372 (6); 17484 (6); 17770 (9); 18421 (9); 20366 (6); 21526 (6). Little, E. L., Jr. 8876 (6); 13094 (6). Lloyd, F. E. 164 (6). López F., M. 1637 (9). Lozano C., G. 2972 (6); 3774 (6); 3911 (19); 4967 (2); 5449 (2). Lugo S., H. 1749 (2). Luna, A. 48 (9). Lundell, C. L. 6232 (9); 6372 (9); 6799 (9); 16300A (9); 18226 (9). Luteyn, J. L. 3335 (11); 8738 (2); 11542 (6); 12690 (10); 12698 (6).

Maas, P. J. M. 12811 (16). Macbride, J. F. 5760* (7). MacDougal, J. M. 3719 (2). MacDougall, T. 565S (9). Madison, M. T. 4519 (2); 4700 (10). Maguire, B. 24009 (15); 28522 (6); 35287* (6); 35296 (6). Makrinus, E. 727 (8). Marcano B. 70-2-77 (15). March 1490 (9). Marín 2192 (6). Martens, P. 7076 (6). Martinelli, G. 9593 (6). Martínez S., E. M. 7969 (9); 15074 (9); 15574 (9); 15589 (9); 16660 (9); 18806 (9); 22911 (9); 22922 (12); 22953 (12). Martínez C., G. 3075 (9). Matuda, E. 17722 (9). Maxon, W. R. 2958 (9); 7501* (10); 8045* (10). McDaniel, S. 14422 (9); 25763 (16). McPherson, G. 6858 (10); 7138 (10); 8328 (11); 8941 (10); 10577 (11); 11846 (10); 13407 (6); 13449 (6). Meclinors 35 (15). Mejía, M. 299 (6); 4995 (6); 23929 (9); 35780 (9); 35781 (6). Mello B. 3605 (6); 5091 (6). Menéndez L., F. 85 (9). Miers, J. 4023 (6). Miller, J. S. 5999 (6). Molina, A. 17169 (12); 17259 (10). Morales, G. 528 (6). Moreira, C. 53 (6). Moreno, P. P. 8510 (11); 16513 (11); 18806 (12); 19112 (9); 19689 (12); 19852 (12); 23735 (9); 24904 (11); 24936 (11). Mori, S. 4873 (11); 5815 (10); 5947 (10); 6095 (11); 6500 (10); 7559 (11); 13292 (6). Morley, B. D. 917 (9). Morton, C. V. 3219 (9). Moya, S. 106 (6). Mutis, J. C. 3655 (2).

Nash, G. V. 1753 (6). Nee, M. 18764 (9); 22719 (9); 24986 (9). Neill, D. 382 (11); 1924 (9); 7259 (9).

Oldeman 38 (6). Orozco, J. M. 142 (11). Otero, J. I. 639 (6). Ownbey, M. 2669 (2); 2737 (5).

Palacios, W. 4433 (15); 6540 (5). Pennell, F. W. 5890 (2); 5898 (6). Pinto E., P. 6233A (15). Pittier, J. 3190* (12); 6594 (16). Plowman, T. 2862 (6); 13370 (6). Pounds, W. Z. 221 (11). Poveda, L. J. 1664 (11). Prance, G. T. 9436 (6); 29385 (6). Primack, R. 363 (11); 403 (11). Proctor, G. R. 16999 (6); 17634 (6); 22567 (9); 32634 (9). Purpus, C. A. 262* (12).

Quentin, R. P. 488 (6). Questel, A. 1628 (6); 2257 (6); 4756 (6).

Ramiz G. 503 (6). Reitz 1825 (6); 2058 (6); 5789 (6). Reko, B. P. 6 (9). Restrepo 449 (2). Revilla, J. 576 (16); 858 (15). Riedel 1240 (6). Robinson, J. W. L. 200 (2). Robleto, W. 138 (9). Rodríguez, L. 2739 (6); 4454 (6); 4460 (6). Roig, J. T. 6104 (9); 6650 (9). Romero C., R. 6753 (6); 7010 (6); 7027 (6); 7803 (6). Rovirosa, J. N. 577 (9). Rusby, H. H. 863 (6).

Sagástegui A., A. 5997 (1). Samp, A. 6896 (6). Sánchez, V., J. G. 317 (1). Sandeman, C. 3672 (5). Sargent, F. H. B155 (6); 590 (6). Sastre, C. 1934 (6). Schipp, W. A. S-585 (9). Schultes, R. E. 13030 (15); 13075* (16). Schunke, C. A100 (7); 290 (6); 436 (7). Schunke V., J. 4458 (16); 4784 (16); 5247 (6); 5317 (6); 7672 (6); 8170 (6); 8380 (3); 10292 (15); 11391 (6). Seibert, R. J. 495 (10). Seifritz, W. 1038 (9). Sello 1754 (6); 5988* (15). Shafer, J. A. 3137 (9); 3297 (6); 3443 (6); 3619 (6); 8004 (6); 8551 (9). Silva, N. T. 927 (15). Simpson, D. R. 806 (15). Sintenis, P. 151B (6); 525 (6); 1609 (6). Slane, V. 607 (6). Smith, A. 120 (11); 2737 (12); 2678 (11). Smith, A. C. 10256 (6); 10549 (6). Smith, D. N. 4139 (6); 4385 (5); 6323 (6). Smith, H. H. 725 (6); 1654 (6). Solomon, J. C. 10826 (6); 13957 (15). Spellman, D. 1639 (9). Spruce, R. 5079 (6); 6186*

(2). Standley, P. C. 38472 (10); 42187 (10); 42599 (10); 42771 (10); 44733 (10); 44738 (11); 46152* (8); 50144 (10); 50691 (10); 52736 (9); 54583 (9); 55581 (9); 68706 (9); 84616 (9); 84893 (9); 91610 (12). Steere, W. C. 8070 (6); 8196 (6). Stehlé, H. 187 (6); 334 (6); 429 (6); 868 (6); 4688 (6); 6005 (6); 6060 (6); 7406 (6); 8115 (6). Stein, B. A. 3108 (2); 3564 (6). Steinbach, J. 9026 (6). Stevens, W. D. 5628 (11); 5947 (11); 6552 (12); 7404 (9); 9616 (11); 11558 (11); 11679 (11); 23919 (12); 24389 (12); 24958 (13); 25120 (13). Steyermark, J. A. 381 (6); 1140 (6); 31627 (12); 33183A (9); 33502 (9); 35211 (9); 33667* (8); 36731 (9); 37255 (9); 39464 (9); 44195 (12); 44435 (9); 46048 (9); 46606 (9); 46808 (9); 47954 (9); 52827 (2); 54093 (6); 55808 (6); 56156 (6); 56591* (6); 59799 (6); 61433 (15); 62044 (6); 75974 (6); 88052 (15); 88835 (15); 93882 (6); 94089 (6); 94645 (6); 99274* (19); 99777 (19); 103708 (6); 104445 (6); 106214 (6); 106453 (6); 116874 (6); 122876* (19); 123255 (19). St. Hilaire B2243 (6). Stimson, W. R. 1870 (6). Sturrock 460 (6). Sugden, A. M. 217 (19); 1026 (6). Sutton 218 (9).

Tate, G. H. H. 710 (6). Taylor, C. M. 6353 (6); 10445 (6). Taylor, N. 519 (9). Terborgh, J. 357 (6). Tessene, M. F. 1377 (11). Tessmann, G. 4020 (6). Timaná, M. 823 (5); 827 (5). Ton, A. S. 3853 (8). Tonduz, A. 17755 (10). Tuerckheim, H. von II340 (9); II2254 (9); 7920 (9). Tyson, E. L. 3436 (11).

Ule, E. 4422 (6); 6305* (16); 15737 (16). Uribe U., L. 3197 (2). Utley, J. 2609 (11); 5223 (11).

Valdivia Q., P. 766 (9); 951 (9); 1423 (9). Valerio R., J. 1359 (8). Vareschi 4771 (6). Vargas, C. 15615 (6). Vásquez, R. 4116 (3); 4130 (15); 6421 (15); 10091 (15); 11879 (16). Vaught 305 (8). Vauthier, M. 77 (6); 96 (6). Vélez, I. 786 (6). Ventura A., F. 20644 (9).

Wadsworth, R. K. 443 (6); 492 (6); 617 (6). Wagner, R. J. 176 (6); 1680 (6); 1752 (6). Webster, G. L. 209 (9); 13239 (6); 15378 (9). Weddell, M. 1520 (6). Wendt, T. 2775 (9); 4451 (9); 5779 (9). Werff, H. van der 6722 (10). Weston, A. S. 10198B (11). Wilbur, R. L. 7389 (6); 7816 (6); 7845 (6); 7947 (6); 16929 (11); 19782 (11); 29803 (11). Williams, Ll. 99 (15). Williams, L. O. 7916 (6); 13068 (9); 15135 (9); 28129 (10); 41950 (8). Williams, R. S. 1478 (6); 11003 (6). Wilson, P. 172 (6). Wingfield, R. 6647 (6). Woytkowski, F. 8236 (1). Wright, C. 125B (6); 266 (9); 1256 (6). Wurdack, J. J. 1027 (1).

Zak, V. 3788 (7). Zamora, N. 619 (11). Zanoni, T. 12914 (6); 18867 (6); 19853 (6); 21127 (9); 22508 (6); 24771 (9); 26660 (6); 35437A (6); 35961 (9). Zarucchi, J. L. 1885 (15); 4168 (2); 5659 (6).

SYSTEMATICS AND EVOLUTION OF THE GENUS *PETREA* (VERBENACEAE)[1]

Ricardo M. Rueda[2]

Abstract

Fourteen of the 35 previously accepted species of *Petrea* L. (Verbenaceae) are accepted in the present revision, three known only as fossils. Morphological, anatomical, and ecological characteristics of the species of *Petrea* are presented, along with descriptions, illustrations, and distribution maps. A cladistic analysis of the tribe Petreeae Briq., using *Citharexylum* L. and *Duranta* L. for outgroup comparison, revealed that *Petrea* is most closely related to *Xolocotzia* Miranda. *Xolocotzia* was then used as an outgroup to polarize the character states within *Petrea*, resulting in a cladogram with a consistency index of 0.74 and a retention index of 0.86, after three rounds of successive weighting.

Resumen

El número de aceptadas especies en el género *Petrea* L. (Verbenaceae) fue reducido de 35 a 14; tres son sólo conocidas de fósiles. Características morfológicas, anatómicas, y ecológicas de las especies de *Petrea* son presentadas, junto con descripciones, ilustraciones, y mapas de distribuciones. En el análisis cladístico de la tribu Petreeae Briq., se usó como grupo externo *Citharexylum* L. y *Duranta* L.; este análisis reveló que *Xolocotzia* Miranda es el más cercano evolutivamente al género *Petrea*. *Xolocotzia* fue usado como grupo externo para polarizar el estado de los caracteres dentro de *Petrea*, resultando un cladograma con un índice de consistencia de 0.74 y un índice de retención de 0.86, después de tres corridas de revalorización de los caracteres.

Petrea L. is a poorly known genus of the Verbenaceae. The most recent taxonomic treatment was written by Moldenke (1938). This monograph has long been outdated, making identification of the species difficult. A considerable number of discrepancies have been found between the characters used in the keys and those given in the individual descriptions of the species. Moreover, additional collections and new species described since 1938 have rendered the keys obsolete.

Moldenke (1938) included 29 species in *Petrea*, and six additional species were described later, one as a preliminary part of the present study (Rueda, 1992). *Petrea*, as interpreted here, contains 14 species, three of which are known only from fossils.

The extant species are exclusively neotropical,

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growing in diverse habitats such as riparian forests and savannas and on soil types such as white sand and limestone. The species range from southern Mexico through Central America and the West Indies to Bolivia, Paraguay, and Brazil, being most diverse and concentrated in northern Brazil and the Guianas. Fossils are known from the former Czechoslovakia, Colorado, and California. One species is widely cultivated in warm and temperate regions of the world.

Petrea possesses three distinctive features: usually asperous leaves, an enlarged persistent calyx that provides wings for wind dispersal or flotation for water dispersal, and a calycinal crest that protects the corolla in prefloration and protects the ovary after the corolla falls. A cladistic assessment of both inter- and intrageneric relationships was made using data on gross morphology, anatomy, and ecology. While many characters in *Petrea* are unique to the genus, and thus useful systematically only within the genus, the polarity of others can be ascertained by using the monotypic Mesoamerican genus *Xolocotzia* as an outgroup. *Petrea*, as a genus, is cladistically defined by the presence of a calycinal crest.

History of the Genus

The first known reference to a plant belonging to *Petrea* was in 1736 when Philip Miller gave Linnaeus unpublished Houstoun notes entitled *Houstounia Genera Plantarum Americanarum Nova Communicata* (Stafleu & Cowan, 1979), in which was included the name *Petrea*. This name was used by Houstoun to accommodate the single species *P. volubilis* L. He named the genus after Robert James Petre, a famous English collector of living plants (Moldenke, 1938). The name was first published by Linnaeus in his *Genera Plantarum* (1737), and *Petrea volubilis* appeared in his *Species Plantarum* (Linnaeus, 1753). The material of this species came from a cultivated plant in Europe which had been brought from Veracruz, Mexico.

Petrea is a distinctive genus in the Verbenaceae and its delimitation has never been a problem. Indeed, Agardh (1858) placed *Petrea* in its own family, but other authors have uniformly included it in Verbenaceae, although its placement within the family has been debated. Schauer (1847) placed it in his seventh subtribe, the monogeneric Petreae, in the tribe Verbeneae Dumort. Bentham & Hooker (1876) placed it in the tribe Verbeneae along with such diverse genera as *Baillonia* Bocq., *Casselia* Nees & Mart., *Citharexylum* L., *Duranta* L., *Ghinia* Schreber, and *Verbena* L. For Briquet (1895) the tribe Petreeae was part of the subfamily Verbenoideae and comprised two genera, *Casselia* Nees & Mart. and *Petrea* L. Junnel (1934), in one of the most recent studies of the phylogeny of the family, reverted to Schauer's original system and treated *Petrea* as constituting a separate subtribe in the tribe Verbeneae.

After Linnaeus's (1753) publication of the genus, along with its first species, nothing was published about *Petrea* for more than 60 years. In the nineteenth century, however, new species were described by Humboldt, Bonpland & Kunth (1818) and Schauer (1847). Pittier (1925) described an additional new species. In 1938, Moldenke published the first modern monograph of the genus, including several new species. Unfortunately, his study was based solely on herbarium material, and many of the species he described have proven to be variants due to cultivation or environmental factors.

Since Moldenke's (1938) monograph, taxonomic work on *Petrea* has consisted entirely of local floristic treatments (MacBride, 1960; Gibson, 1970; Moldenke, 1973) and isolated publications of new species, mainly by Moldenke. The last new species published before this study was *P. sulphurea* Jansen-Jacobs, in the treatment of the Verbenaceae of French Guiana by Jansen-Jacobs (1988).

Morphology

The species included in *Petrea* share unique characteristics (e.g., calycinal crest, winged calyx), which have made the phylogenetic placement of the genus in the family difficult. In the discussion of morphological characteristics of *Petrea* given below, the degree of variation for each character is presented, as well as an evaluation of the importance of each character in the taxonomy of the genus.

Habit

All *Petrea* species are woody, ranging from lianas and shrubs to trees. The habit in *Petrea* seems to be very plastic, and individuals of the same species can be a liana, shrub, or tree as in other scandent Verbenaceae. Putz (1982) found that *Aegiphila cephalophora* Standl. grows as a liana in the forest but as a small shrubby tree in the open. The ability of the species of the genus to reproduce vegetatively by sprouting from stumps was confirmed by field observations.

Roots

The root system of *Petrea* species consists of a radiating array of shallow white roots, with an

abundance of periderm that falls off easily. Excluding two collections (*Croat 9432* and *Hammel 1868*) from Panama that report *Petrea* as an epiphyte, all the species of *Petrea* have been found to be rooted in the ground. Stems of *Petrea* root easily; stems that are forced to the ground during a treefall root and give rise to new shoots that may later become independent individuals.

STEMS

The stems of *Petrea* species are mostly slender, whitish, grayish, or brownish in color, with conspicuous lenticels, and may be glabrous or asperous. A cross section of the stem of *Petrea* shows four or five thick rays going to each of the furrows, and this can be used to identify the genus vegetatively. However, in many species the stem is cylindrical and the rays are equal in thickness, making it more difficult to distinguish the genus. Stems of the tree species tend to be irregular and oval in shape. In lianas the stem is sometimes four-angled and/or furrowed. According to Carlquist (1988), *Petrea* has only a single cambium, situated in the normal position between the xylem and the phloem; furrowed stems are formed because the cambium is not equally active around the whole periphery of the axis. In its simplest form, the cambium irregularly produces axes that are oval or elliptic instead of circular, e.g., in *Petrea pubescens* Turcz. In more extreme forms, the stem can be strongly furrowed, as sometimes occurs in *Petrea volubilis* L.

PUBESCENCE

Nine distinct hair types (see Table 1) were found in *Petrea* and *Xolocotzia*:

(1) Conic hairs are the most abundant type of hairs on the surfaces of the leaves. These hairs are called silicified conical papillae by Metcalfe & Chalk (1972) and have only been found in *Petrea* and *Xolocotzia*. They are short, broad-based, conical-tipped, unicellular, silicified and make the leaf rough to the touch. These hairs are an outgrowth of the epidermis, where they are found in shallow depressions (Fig. 1A, B).

(2) Bulbous hairs (Moldenke, 1938) are found on upper leaf surfaces and sometimes on bracts and petioles of *Petrea* and *Xolocotzia*. These hairs are bulbous at the base (Fig. 1C, D). They are rarely found in older leaves, apparently because they break and fall off with age.

TABLE 1. Types of hairs and plant parts and where they occur in *Petrea* (P) and *Xolocotzia* (X).

Hair type	Petiole	Leaf	Bract	Calyx	Corolla	Pedicel
Bulbous	PX	PX	PX			
Clavate glandular	P	P	P	P	P	P
Clinate	P	P	P			P
Conic		PX				
Falcate	X					
Lageniform				PX		
Ribbon					PX	
Subsessile glandular		PX				
Warty					P	

(3) Clinate hairs (sensu Hewson, 1988) are more common than bulbous on the different structures of *Petrea* and *Xolocotzia*. These hairs grow at an angle of 45° with the surface on which they are found.

(4) Subsessile glandular hairs (Abu-Asab & Cantino, 1987) are common on lower leaf surfaces and fewer in number on upper surfaces, where they are sunken. While subsessile glandular hairs may appear sessile in surface view, a short, usually discoid stalk cell may be seen in cross section (Abu-Asab & Cantino, 1987). The subsessile glandular hairs can be single-celled as in *P. sulphurea* or multicellular as in *P. pubescens*. Puff (1978) also reported stalked glandular hairs on the leaves of *P. volubilis*, but they were not observed in this study.

(5) Falcate hairs (sensu Payne, 1978) have the tip curved and are only found on petioles of *Xolocotzia*.

(6) Clavate glandular hairs (Abu-Asab & Cantino, 1987) occur on leaves but are more common on calyces and corollas of *Petrea*. Clavate glandular hairs are spherical-headed with a long unicellular stalk. The head is yellowish and consists of several radially arranged secretory cells.

(7) Lageniform hairs (sensu Payne, 1978) are

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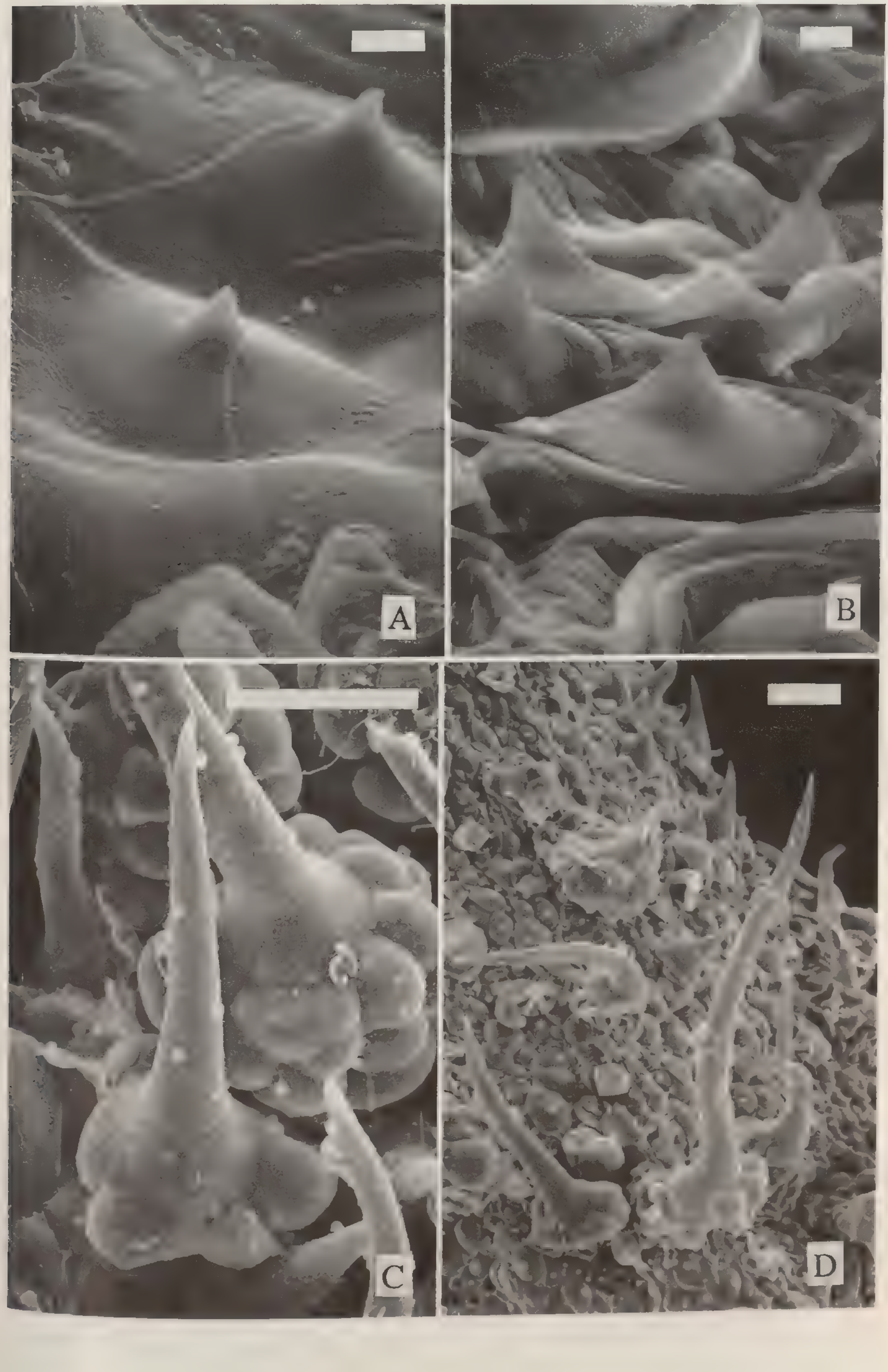
FIGURE 1. Pubescence in the genera *Petrea* and *Xolocotzia*.—A. *P. bracteata* (*Rueda & Ruiz 590*), B. *X. asperifolia* (Neill 5477), showing conic hairs found on leaves.—C. *P. blanchetiana* (*Martius 1029*), D. *X. asperifolia* (*Neill 5477*), showing bulbous hairs found on leaves, bracts, and petioles of *Petrea* and *Xolocotzia*. (SEM photos; bars in A, B = 50 μm, C, D = 5 μm.)


A
B
C
D

found on the calyx of *Petrea* and *Xolocotzia*. They are flask-shaped hairs.

(8) Ribbon hairs (sensu Payne, 1978) are found on the calyx and corolla of *Petrea* and *Xolocotzia*. These hairs are shaped like a flowing ribbon.

(9) Warty hairs (sensu Hewson, 1988) are found in the interior of the corolla of *Petrea*. These hairs are covered with wartlike protuberances (Fig. 2A, B). They may help retain pollen close to the stigma.

LEAVES

Leaves are highly variable in size and texture, even within species. They often feel like sandpaper. This roughness is due to the presence of special hairs found on the surface(s) of the leaves (see Pubescence). The underside of the leaves is useful in separating species. Pitted leaves (Fig. 2C) are only present in *P. brevicalyx* Ducke, *P. campinae* Rueda, and *P. macrostachya* Benth., whereas bullate leaves (Fig. 21B) are only present in *P. rugosa* Kunth. All other species have the leaves smooth underneath (Fig. 2D). Leaf texture is useful as a taxonomic character, although it is in some cases difficult to define except on a comparative basis.

Leaves of *Petrea* are uniformly simple and opposite or whorled. Some species are characterized by verticils of three or four leaves. However, other species may have 90% of the leaves decussate and 10% verticillate, while others show the opposite percentage.

Venation patterns are not useful in separating species because all are brochidodromous (Hickey, 1979), with the angle formed by the secondary veins and the midrib and the anastomosing of the veins near the margin similar in all species. The tertiary venation is variable and densely netted. This type of venation is common in other verbenaceous genera, such as *Aegiphila*, *Citharexylum*, *Cornutia*, and *Duranta*.

Stomatal patterns have proven to be useful taxonomically (Cantino, 1990), and three groups of species may be recognized within *Petrea*. Stomata were observed and photographed with an S-450 scanning electron microscope (SEM). Additional observations were made with the plastic imprint technique of Sinclair & Dunn (1961), and classification of stomata follows Cantino (1990). Three basic types of stomata were found in the genus (see Table 2). The type of stomata is not helpful at the species level. However, the type of stomata can be useful for making groups. Thus, the anomocytic type (Fig. 3A) is present in species such as *P. brevicalyx* and *P. insignis* Schauer; diallelocytic stomata (Fig. 3B) occur in *P. pubescens*, *P. rugosa*, *P. sulphurea*, and in *X. asperifolia* Miranda (outgroup). The paracytic type (Fig. 3C) is found in *P. blanchetiana* Schauer, *P. maynensis* Huber, and *P. volubilis*.

POLLEN

Pollen of *Petrea* is characteristic of the genus but has little interspecific differentiation. Scanning electron micrographs show that pollen of all species is more or less triangular and tricolpate. The ornamentation of the exine of all species is psilate or smooth without sculpturing (Fig. 3D). The pollen in *Xolocotzia* (outgroup) differs from that of *Petrea* in being more spherical and in having a reticulate exine (Fig. 3E).

FRUITS AND SEEDS

The fruit of *Petrea* is drupaceous and enclosed by the calyx. The accrescent fruiting calyx, which encloses the fruit, usually has the same color as the flowers, but sometimes becomes green (e.g., *P. volubilis*). The lobes do not change much in shape but become stiffer and harder with maturation, forming a near right angle with the tube. The fruit, once out of the calyx, shows remnants of the style on one end and remnants of the receptacle on the other end. The exocarp is leathery or fleshy; the endocarp is hard and bony, 2-celled, and forms two stones. The stones are not easy to separate, and each has one seed. However, sometimes, as in *P. blanchetiana*, there is only one seed found in the fruit. Seeds are laterally or apically attached, and lack endosperm. None of these characters are helpful in separating species or groups of species.

ANATOMY

Anatomical studies were carried out for the distinct parts of the plants. Fresh samples of primary stem, wood, and leaf were collected in 70% ethanol for anatomical studies. Three samples from different individuals of each species were dehydrated in

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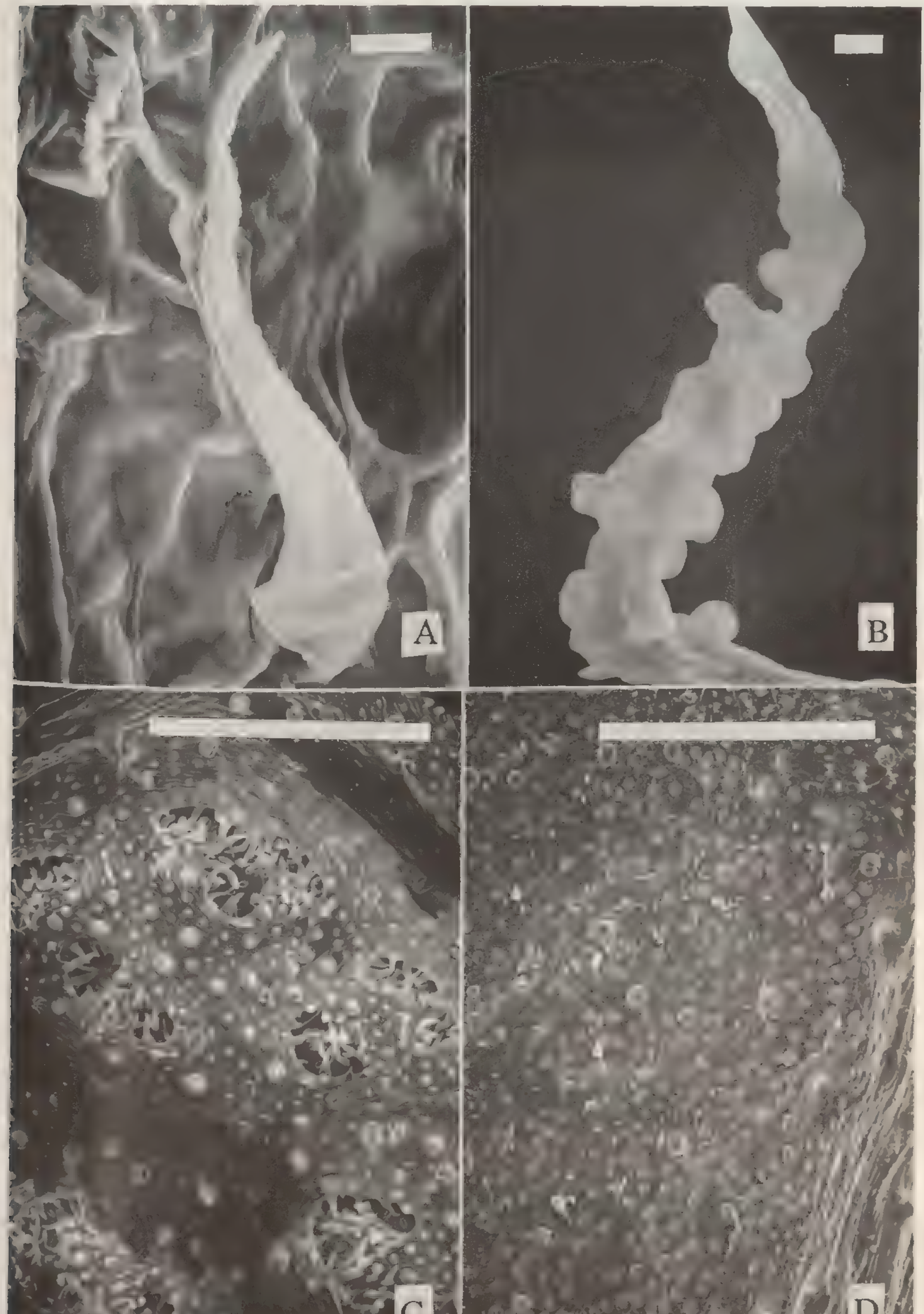
FIGURE 2. Pubescence and leaf surface in the genus *Petrea*.—A. *P. volubilis* (*Gimate 911*), B. *P. macrostachya* (*Jansen-Jacobs et al. 341*), showing warty hairs present in the interior of the corolla.—C. *P. macrostachya* (*Pipoly 7588*), showing a pitted leaf surface.—D. *P. maynensis* (*White 860*), showing a smooth leaf surface. (SEM photos; bars in A = 5 μm, B = 50 μm, C, D = 500 μm.)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D

a series of increasing concentrations of ethanol, embedded in Paraplast, and sectioned on a rotary microtome set at 10–15 μm. Staining was carried out using Johansen's (1940) Safranin-Fast Green technique. Longitudinal and cross sections of shoot apices were stained using the zinc chloride technique (Sharman, 1943) to better discern meristematically active areas.

For taxa available only from herbarium specimens, material was placed in a vial with deionized water and wetting agent and left in a 60°C oven overnight. The material was then washed and stored in 70% FPA and subsequently prepared as described above. All leaves used for clearing studies were obtained from herbarium specimens. The leaves were placed for one day in water to which Aerosol-OT was added, then transferred to a 5% NaOH solution for one week. The leaves were then rinsed with water and placed in 5.25% $NaHCO_3$ (commercial laundry bleach) for one hour. After an ethanol dehydration series, staining was carried out using a 0.5% solution of safranin in 95% ethanol (Johansen, 1940). The trichomes were examined and compared for all the species using light and scanning electron microscopes.

Most of the stem samples were collected from herbarium specimens. These were soaked in equal parts of 60% ethanol and glycerin for three months. The samples were frozen using a Super Histo-Freeze, an appropriate method when stem samples are less than one inch in diameter (R. Keating, pers. comm.), and then slides were made in cross, radial, and tangential section using an 860 American Optical sliding microtome set at 15–25 μm. Section stems were then stained by covering the samples with Johansen's safranin for two hours, followed by rinsing in an ethanol series (Johansen, 1940).

PRIMARY STEM ANATOMY

The anatomy of the primary stem was studied in two species of the genus, *Petrea pubescens* (a tree) and *P. maynensis* (a liana). Lianas and trees show exactly the same histological zones. From outside to inside these zones are: epidermis, cortical zone, stelar zone, and the pith. The epidermis is one cell thick and decorated with 2–3 types of hairs. The cortical zone and stelar zone do not show any special features. The pith is composed of parenchyma cells with no observable special features.

LEAF ANATOMY

In the study of leaf histology three samples of each species of *Petrea* were obtained. The numbers of cell rows forming the epidermis and the number of palisade layers were found to be good characters for species grouping (Table 3). *Petrea campinae* has four rows of epidermal cells, *P. brevicalyx*, *P. macrostachya*, and *P. maynensis* have two rows, and all other species have only a single row. The mesophyll of the leaf of *Petrea* has a palisade tissue consisting of one to several layers of cells, confirming the earlier observations of Metcalfe & Chalk (1972). Sclerenchymatous fibers are present in the mesophyll, and crystals of different sizes are found in the parenchymatous tissues. The vascular bundles of the larger and smaller veins are accompanied by sclerenchyma.

The petiole has a median vascular strand consisting of an almost closed cylinder of xylem surrounded by completely closed cylinders of phloem and fibers. The number of petiolar lateral traces varies among species. Thus, *P. insignis* has no lateral traces, *P. blanchetiana*, *P. macrostachya*, and *P. maynensis* have four lateral traces, and all the remaining species have only two lateral traces.

TABLE 2. Types of stomata found in extant *Petrea* and *Xolocotzia*.

Taxon	Stomatal type		
	Anomocytic	Dialle-locytic	Para-cytic
Petrea bracteata	X		
P. brevicalyx	X		
P. campinae	X		
P. insignis	X		
P. macrostachya	X		
P. pubescens		X	
P. rugosa		X	
P. sulphurea		X	
Xolocotzia		X	
Petrea blanchetiana			X
P. maynensis			X
P. volubilis			X

WOOD ANATOMY

The young stems are commonly quadrangular or terete in transverse section, except in *Petrea sulphurea* M. J. Jansen-Jacobs, where they are angular and winged. Mature stems of the species of *Petrea* show growth rings. According to Welle & Détienne (1988), growth rings are formed by the combination of marginal parenchyma and a difference in vessel diameter. The vessels are round to oval in shape, with simple perforations, solitary or in clusters of 2–6, 20–40 per mm^2, with a diameter that varies from 25 to 250 μm. The rays

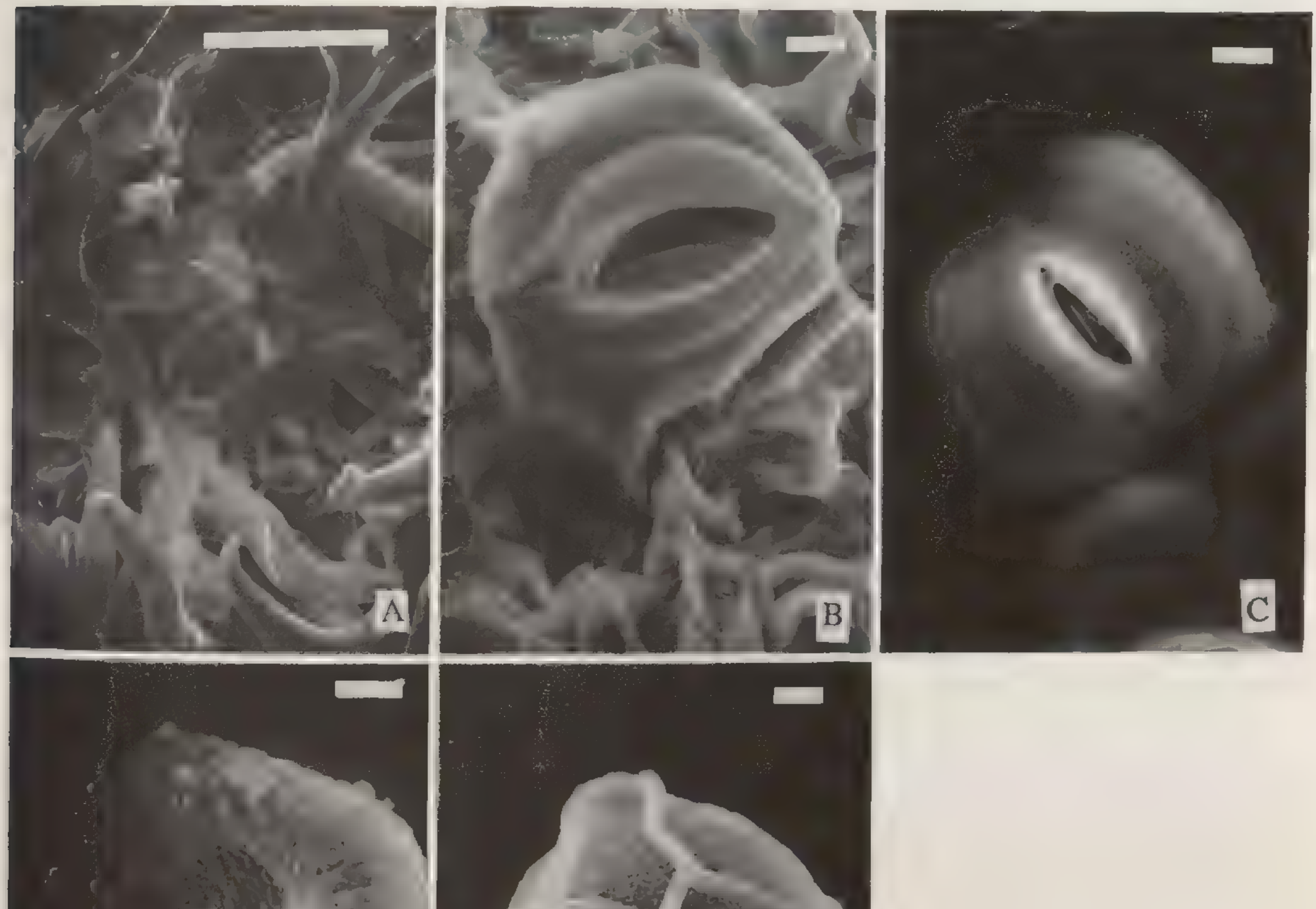


FIGURE 3. Stomata and pollen in the genera *Petrea* and *Xolocotzia*.—A. *P. brevicalyx* (*Ducke 22544*), showing anomocytic stomata.—B. *X. asperifolia* (*Villeda 134*), showing diallelocytic stomata.—C. *P. volubilis* (*Gentry 7794*), showing paracytic stoma.—D. *P. sulphurea* (*Billiet & Jadin 1705*); this triangular-shaped pollen is characteristic of the species of *Petrea*.—E. *X. asperifolia*, with round pollen grains. (SEM photos; bars in A = 50 μm, B–E = 5 μm.)

are uniseriate, as observed in *P. sulphurea*, or multiseriate (1–12 cells wide), as observed in *P. volubilis*. Record & Hess (1941) described the heartwood of *P. arborea* Kunth, now part of *P. volubilis*, as tasteless, odorless, pale orange-brown, and not too well differentiated from the yellowish or light olive sapwood. They also reported distinct ray flecks on radial surfaces. The wood is moderately hard and heavy, medium textured, with straight to finely undulate grain, and has good working properties and fairly high luster. According to Metcalfe & Chalk (1972, 1979), the cork originates superficially and is tabular and thickened on the outer tangential walls. The pericycle contains a composite and continuous ring, and its sclerenchyma includes stone cells as well as fibers. Solitary crystals in the pericycle are associated with the sclerenchyma and are sometimes enclosed within the stone cells.

The wood has silica in all the elements. The fibers are typically septate, but nonseptate in *P. bracteata* and *P. macrostachya*. The pits are mostly simple in the radial walls, but have small borders in some specimens of *P. volubilis*.

TABLE 3. Histological features of the leaves of *Petrea* and *Xolocotzia*.

Taxon	Number of cell rows forming the epidermis	Number of palisade layers	Voucher
X. asperifolia	1	1	*Neill 5477* (MO)
P. blanchetiana	1	1	*Rueda 507* (MO)
P. bracteata	1	2	*Rueda 730* (MO)
P. brevicalyx	2	1	*Ducke 140* (MO)
P. campinae	4	2–4	*Cordeiro et al. 76* (SP)
P. insignis	1	1	*Ducke 688* (MO)
P. macrostachya	2	1	*Smith 2626* (F)
P. maynensis	2	1	*Rueda 1129* (MO)
P. pubescens	1	1	*Rueda 1010* (MO)
P. rugosa	1	2	*García 6472* (COL)
P. sulphurea	1	1	*Billiet & Jadin 1705* (BR)
P. volubilis	1	1	*Rueda 431* (MO)

CYTOLOGY

Number and morphology of chromosomes have not proven to be useful in the separation of species. Two species were studied: *Petrea volubilis* from plants cultivated at the Missouri Botanical Garden that originally came from Central America and Brazil; and *P. blanchetiana* from Peru (*Rueda 615*). All the observations showed a constant chromosome number of $2n = 34$, which is the same result that Goldblatt (1988) reported for *Petrea volubilis*. The chromosome size is also generally invariable. The length of the chromosomes ranges from 1 to 1.5 μm, and the width is less than 1 μm (Fig. 4).

ECOLOGY

HABITAT AND ENDEMISM

The species of *Petrea* are found in the lowlands of the American tropics. Some species are restricted to very specific soil types resulting in narrow endemism. For example, *P. brevicalyx* and *P. insignis* occur primarily in seasonally inundated forest (igapó) in Brazil. *Petrea campinae* is known only from white sand campinas in Roraima, Brazil. Other species have restricted distribution with no obvious ecological correlations. For example, *Petrea macrostachya* is known only from the Guianas but occurs in a wide range of habitat types, including white sand forest. *Petrea volubilis* can be found in many different environments, but it is more common within 300 m of extant or former rivers and in open areas such as gaps or along trails. In general, the distribution of a species often is very patchy even within its habitat, with scattered

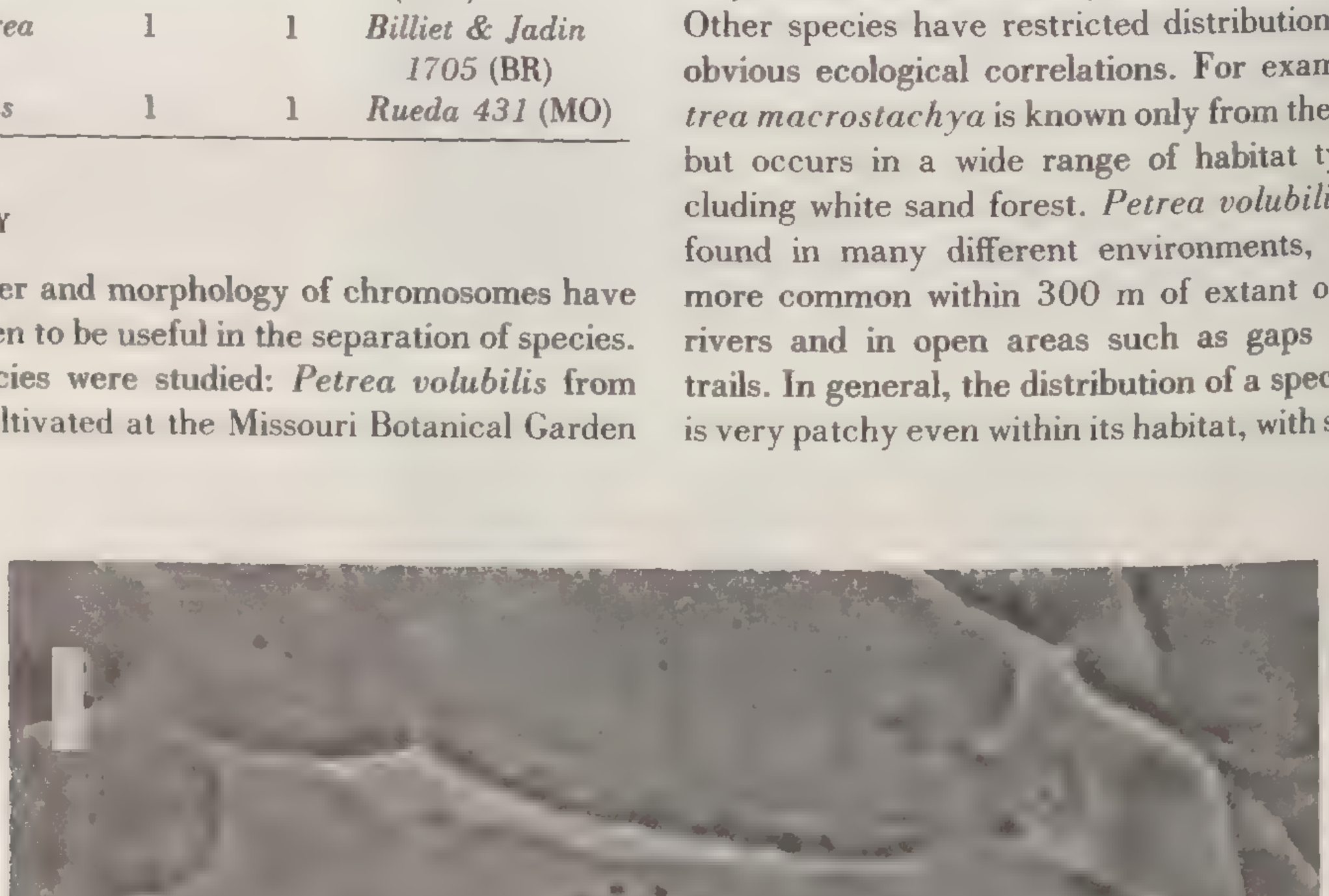


FIGURE 4. *Petrea volubilis* (*Rueda & Cuadros 431*), showing the chromosomes found in the genus *Petrea*. (Bar = 10 μm.)

clumps of six to ten individuals. *Petrea volubilis* can also be found on cliffs. There the rope stems are typically 1–2 cm in diameter and hang 5–6 m, with the leaves grouped at the end, but the inflorescences are upright.

POLLINATION BIOLOGY

Petrea species seem to have a mass-flowering "big bang" phenology at the beginning of their flowering season, but then continue to flower more evenly producing only a few flowers at a time for two or three months. *Petrea blanchetiana* in full bloom was observed to have up to eight groups of inflorescences in 20 m^2, each group with 20 inflorescences, 30–40 cm long, with an estimated 25 30 flowers apiece. Thus *P. blanchetiana* in full flower may produce 4000–6000 flowers in 20 m^2.

The principal visitors to *Petrea* flowers are bees of the tribe Euglossini, although an introduced species of *Apis*, species of *Bombus*, and Heliconiidae butterflies were also observed. Thrips commonly feed on the petals (up to eight counted in a single flower), but they appear to have a negligible role in pollination because they remain in the flowers after the pollen is dry. Euglossine bees are the most commonly observed flower visitors and are, presumably, the most important pollinators of *Petrea*. The most often captured bees in this study were species of *Euglossa*. Individuals of this genus often follow a repeated foraging circuit or "trapline" among successive flowers or clumps of flowers (Janzen, 1971). The sex ratio of these bees at *Petrea* is nearly equal in contrast to the observations of Gentry (1976) in the Bignoniaceae.

The Apinae visitors of *Petrea* were species of *Bombus* and the introduced genus *Apis*. Although *Apis* may now be a significant pollinator of *Petrea*, it is surely not a co-evolved one, since *Apis* has only recently reached the Neotropics.

SEED SET

Fertile fruits appearing swollen or incrassate are easily distinguished from infertile ones, which appear flat. Seed set in *Petrea* is remarkably low, and approximately 80% of flowers abort their ovules. In addition to ovule abortion, predation of fruits limits *Petrea*'s reproductive success. Little predation appears to occur on the plants, but about 40% of the fruits observed found on the ground had been eaten by Curculionidae larvae.

DISTRIBUTION

The 11 extant species of *Petrea* are distributed throughout the Neotropics. They range from southern Mexico (Veracruz) through the West Indies and Central America to Brazil, Paraguay, and Bolivia. The main concentration of species is in northern Amazonia, in Brazil, and the Guianas. *Petrea volubilis* is the "weedy" species of the genus, being found throughout the entire distribution of the genus (Fig. 5). Other wide-ranging species include *P. blanchetiana*, found from Panama, Colombia, and Venezuela south to Peru and southeast to Brazil and the Guianas (Fig. 6); *P. maynensis* occurs from Colombia south to Peru, Brazil, and Bolivia (Fig. 7); *P. pubescens* ranges from Venezuela south to Colombia, Ecuador, and Peru (Fig. 8); *P. bracteata* ranges from the Guianas southwest through Brazil to Amazonian Peru (Fig. 9). *Petrea macrostachya* is endemic to the Guianas (Fig. 10); *P. sulphurea* is known only from French Guiana (Fig. 10); and *P. insignis* is restricted to northern Amazonian Brazil (Fig. 10). *Petrea brevicalyx* and *P. campinae* are endemic to Amazonian Brazil (Fig. 11); *P. rugosa* is endemic to southern Colombia and adjacent Venezuela (Fig. 11). In addition, fossil species are known from the United States and from the former Czechoslovakia (Moldenke, 1938).

USES

The known uses of *Petrea* are limited. In flower or fruit the plants are attractive; they were first grown as an ornamental in 1733 when W. Houstoun brought *Petrea volubilis* into cultivation from Veracruz, Mexico (Aiton, 1812). Most of the species are grown locally; only *P. volubilis* is widespread in cultivation. *Petrea maynensis*, *P. pubescens*, and *P. rugosa* are, at least locally, used in horticulture. *Petrea* plants are easily propagated by cuttings or layering.

Record & Hess (1941) considered the wood of *Petrea* to be poorly resistant to decay and without any commercial value. The wood is very hard to cut when dry and seems to be good as firewood, burning fast, without much smoke (pers. obs.).

There are also scattered reports of the use of *Petrea* as a medicinal plant in the West Indies, Ecuador, and the Guianas. In the West Indies, *P. volubilis* is mixed with *Chiococca alba* (L.) Hitchc., to prepare a tea for use as an abortifacient (Ayensu, 1981). In Ecuador *P. maynensis*, mixed with three other plants, is used as a contraceptive (Wilbert & Neill, 1987). In the Guianas, the ash obtained from the vegetative part of *P. bracteata* is applied to legs to relieve aches and pains (R. DeFilips, pers. comm.).

The pharmacological action of *Petrea* is unknown but Andray et al. (1982) reported phenylpropanoid glycosides in *Petrea* and in more than

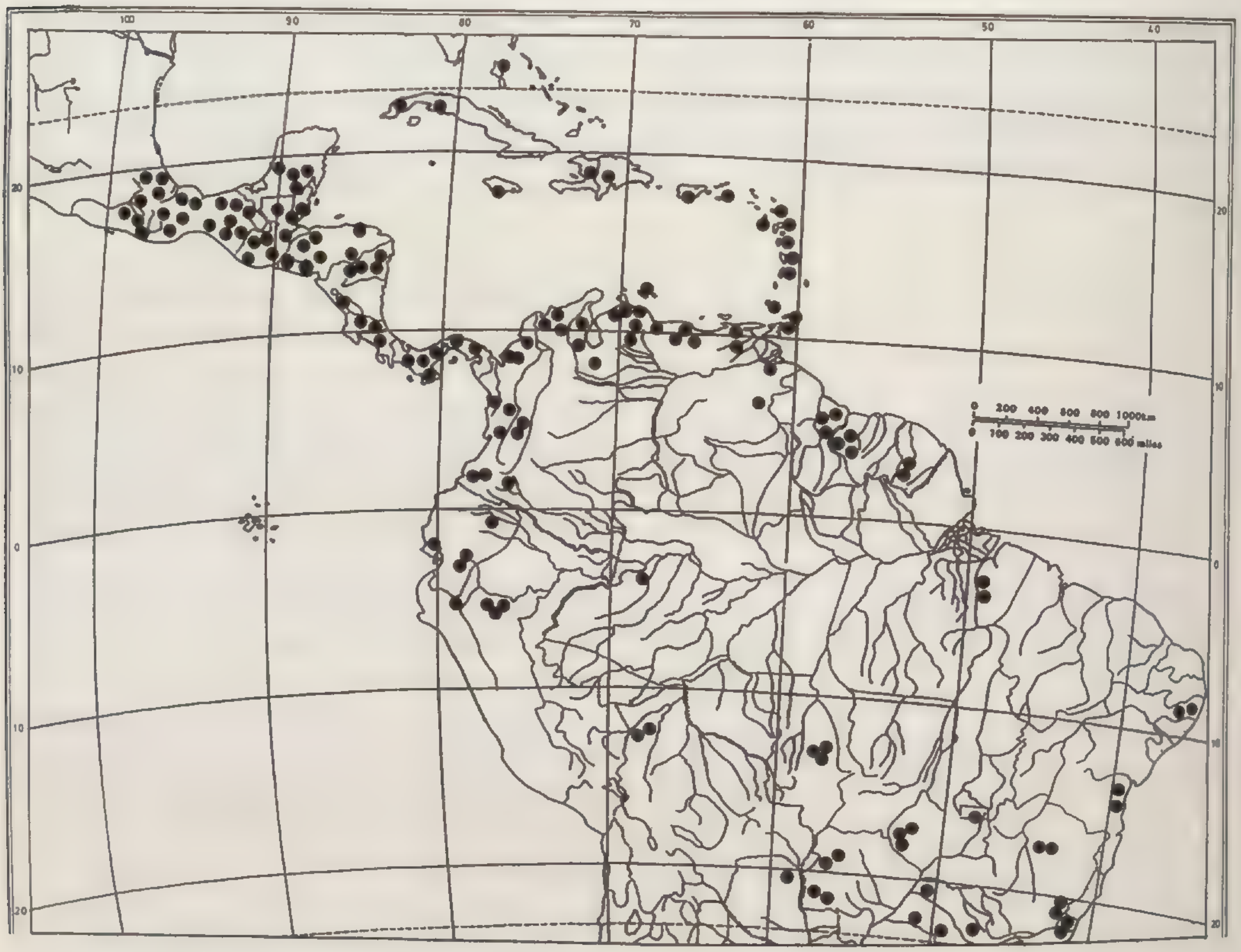


FIGURE 5. Distribution of *Petrea volubilis*.

40 other genera that are used in folk medicine. These compounds have proved to have good antibacterial, antihypertensive, and analgesic properties (Garnier et al., 1989).

Finally, *Petrea rugosa* is used as a melliferous plant for hive honeybees in Medellín, Colombia. Echeverry (1984) also reported that *P. pubescens* and *P. rugosa* are used as melliferous plants in the department of Tolima.

PHYLOGENY

More than 1000 species and about 40 genera of Verbenaceae occur in the New World. *Petrea* has always been considered distinct and separate from other American genera by the calycinal crest present on the calyx and by the asperous leaves. In this treatment, *Petrea* is placed along with *Casselia* Nees & Martius, *Lampaya* F. Philippi, *Recordia* Moldenke, and *Xolocotzia* Miranda in the tribe Petreeae Briq., following Briquet (1895) and Moldenke (1971). Defining characters shared by members of this tribe include fruits with two 1-celled and 1-seeded pyrenes, characters originally used by Briquet (1895) for tribal delimitation.

METHODS

Hypotheses of the phylogenetic relationships of *Petrea* to the other genera in the Petreeae, as well as relationships between the species of *Petrea*, were generated by a cladistic analysis. For the analysis of the tribal as well as species relationships, the distribution of synapomorphies was analyzed using parsimony criterion (minimizing homoplasy; Kaplan, 1984). On the basis of these synapomorphies, taxa were ordered into one or more patterns represented by hierarchical branching patterns. Character polarity for the characters selected was determined by the outgroup comparison method (Maddison et al., 1984). Data were analyzed using Farris's phylogenetic package, Hennig86 (version 1.5; Farris, 1988), applying the implicit enumeration option for calculating trees. In the analysis of *Petrea* characters 2, 4, and 10 were considered unordered. The successive weighting procedure in Hennig86 was also used, which calculates weights from the best fits to the most parsimonious tree, using rescaled consistency (rc), which is the product of the character consistency (c) and the character retention index (r). The product is scaled to lie in the range 0–10. The weighting procedure is re-

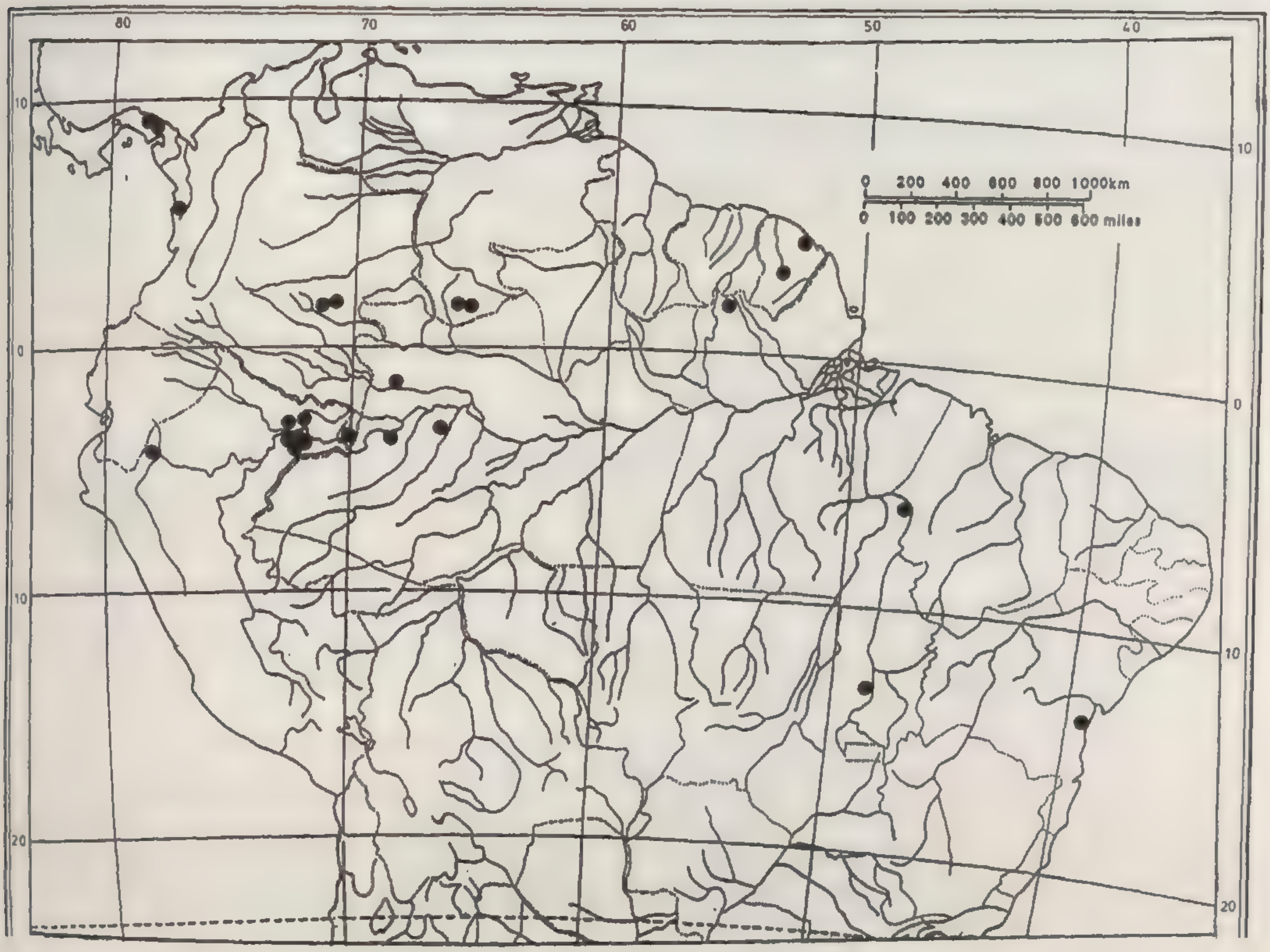


FIGURE 6. Distribution of *Petrea blanchetiana*.

peated on successively produced trees until the trees no longer change (Farris, 1989). The program Clados (version 1.1; Nixon, 1992) was used for examination of character and distributions and production of the figures.

CLADISTIC ANALYSIS OF THE TRIBE PETREEAE

One of the most difficult tasks in attempting a cladistic analysis lies in the choice of appropriate outgroups (Watrous & Wheeler, 1981). However, if outgroups are explicitly designated, the phylogenetic hypothesis can be modified as more data on the relationships of the genera become available. *Citharexylum* and *Duranta* of the tribe Citharexyleae in the subfamily Verbenoideae were chosen for the cladistic analysis of the tribe Petreeae (which is also Verbenoideae). Citharexyleae are clearly delimited in the subfamily by having fruit composed of two or four 2-celled and 2-seeded pyrenes. *Citharexylum* and *Duranta* are well known, making character evaluation less problematic than in some of the other genera of the tribe, where most species and even entire genera are known only from a few collections.

Once the character states were determined and polarized (Table 4), a variety of procedures for hypothesizing relationships were possible. Autapomorphies (characters that occur only in one taxon) were omitted because they are uninformative about taxonomic relationships. However, these autapomorphies were used to define species before running the cladistic analysis. All the characters used were polarized by outgroup comparison with the two members of the Citharexyleae. The only synapomorphy that is shared by the two tribes is the spicate or racemiform, indeterminate, and centripetal inflorescence.

The data matrix for the study of generic relationships is presented in Table 5. A single most parsimonious tree to length 12, consistency index of 0.83, and a retention index of 0.81 was obtained for the subtribe Petreeae. The tree (Fig. 12A) has a basal trichotomy, and *Petrea* and *Xolocotzia* appear as a distinct clade defined by two unique character states, leaves with bulbous-based hairs (Fig. 1C, D) and a lobed calyx. In addition, each genus is defined by its own autapomorphies. *Xolocotzia* is defined by having round reticulated pollen, whereas *Petrea* is defined by having triangular

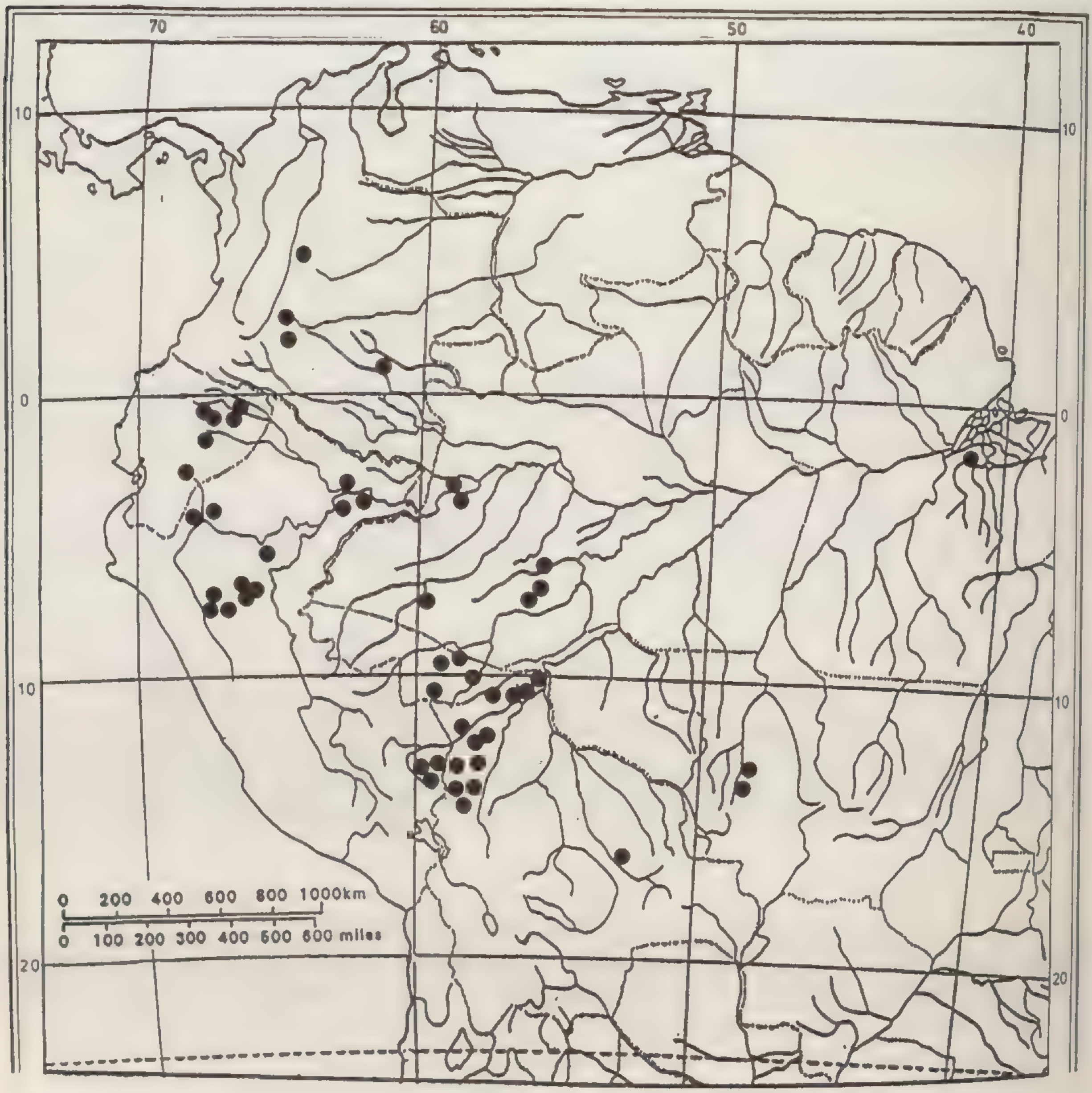


FIGURE 7. Distribution of *Petrea maynensis*.

smooth pollen and a calycinal crest on the calyx. The use of more than one character to infer a common ancestry for this clade does not support the possibility that these relationships are due to homoplasies rather than to homologies.

CLADISTIC ANALYSIS OF THE GENUS *PETREA*

The cladistic analysis conducted to determine hypotheses of relationships among the species of the genus *Petrea* followed the same procedure as that used for the tribe Petreeae. The character states (Tables 6, 7) were polarized using the genus *Volocotzia* as an outgroup. After three rounds of successive weighting, one fully resolved tree of length 122, consistency index of 0.74, and a retention index of 0.86 was obtained (Fig. 12B). The resulting tree shows that *Petrea* is monophyletic and contains the following eight monophyletic groups: (1) comprises all species but *P. insignis*, which is the only species in the genus without lateral traces; (2) *P. maynensis* and *P. volubilis* both with aborted axillary racemes; (3) *P. pubescens* and *P. rugosa*, the only erect species in the genus; (4) all the remaining species except *P. sulphurea*, the species in this clade with a pair of bracteoles on the pedicel; (5) the remaining species except *P. bracteata*, the species in this clade with more than one layer of palisade tissue; (6) all the remaining species except *P. blanchetiana*, the species in the clade with a mesophyll of more than four layers of palisade; (7) the remaining species except *P.*

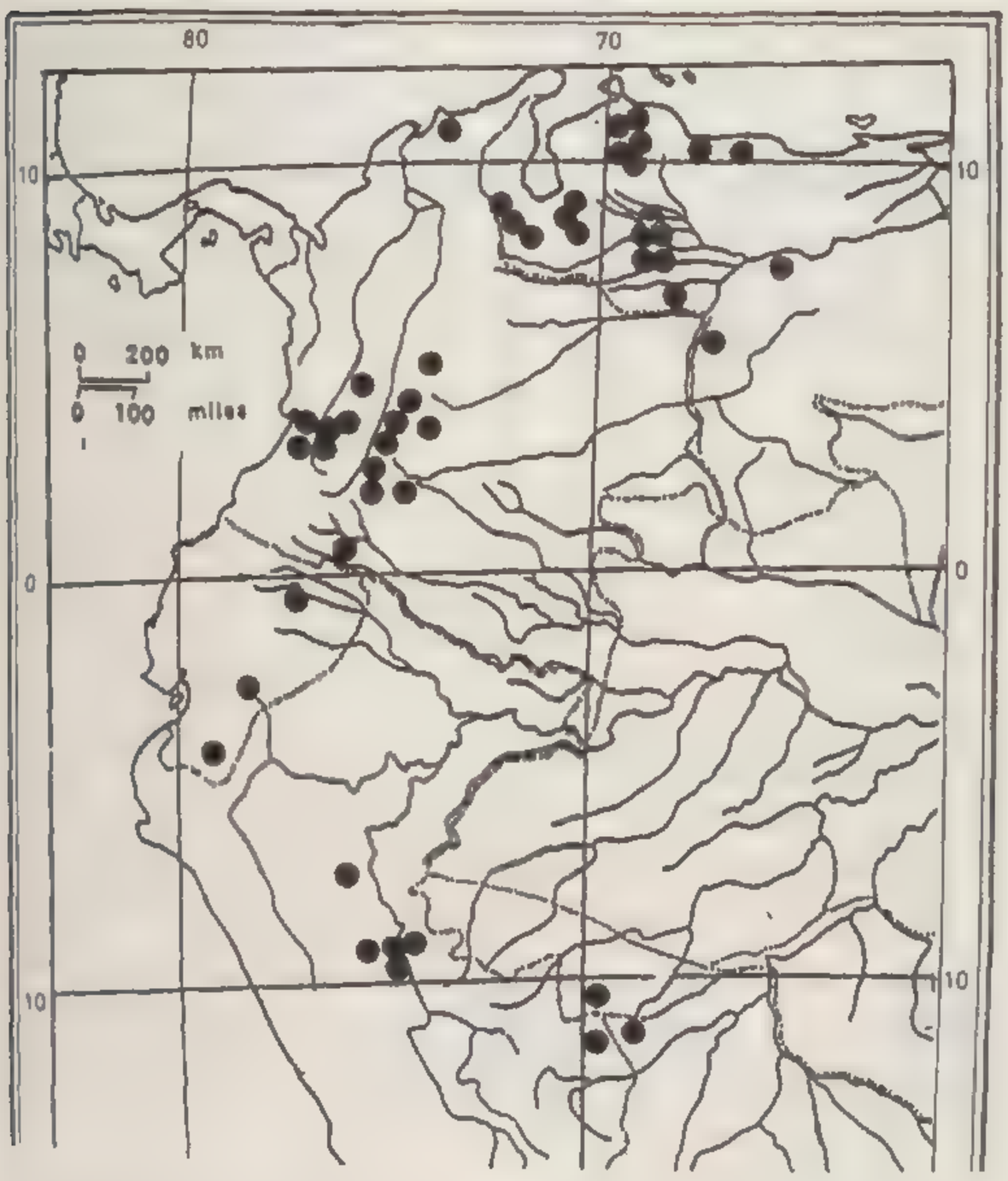


FIGURE 8. Distribution of *Petrea pubescens*.

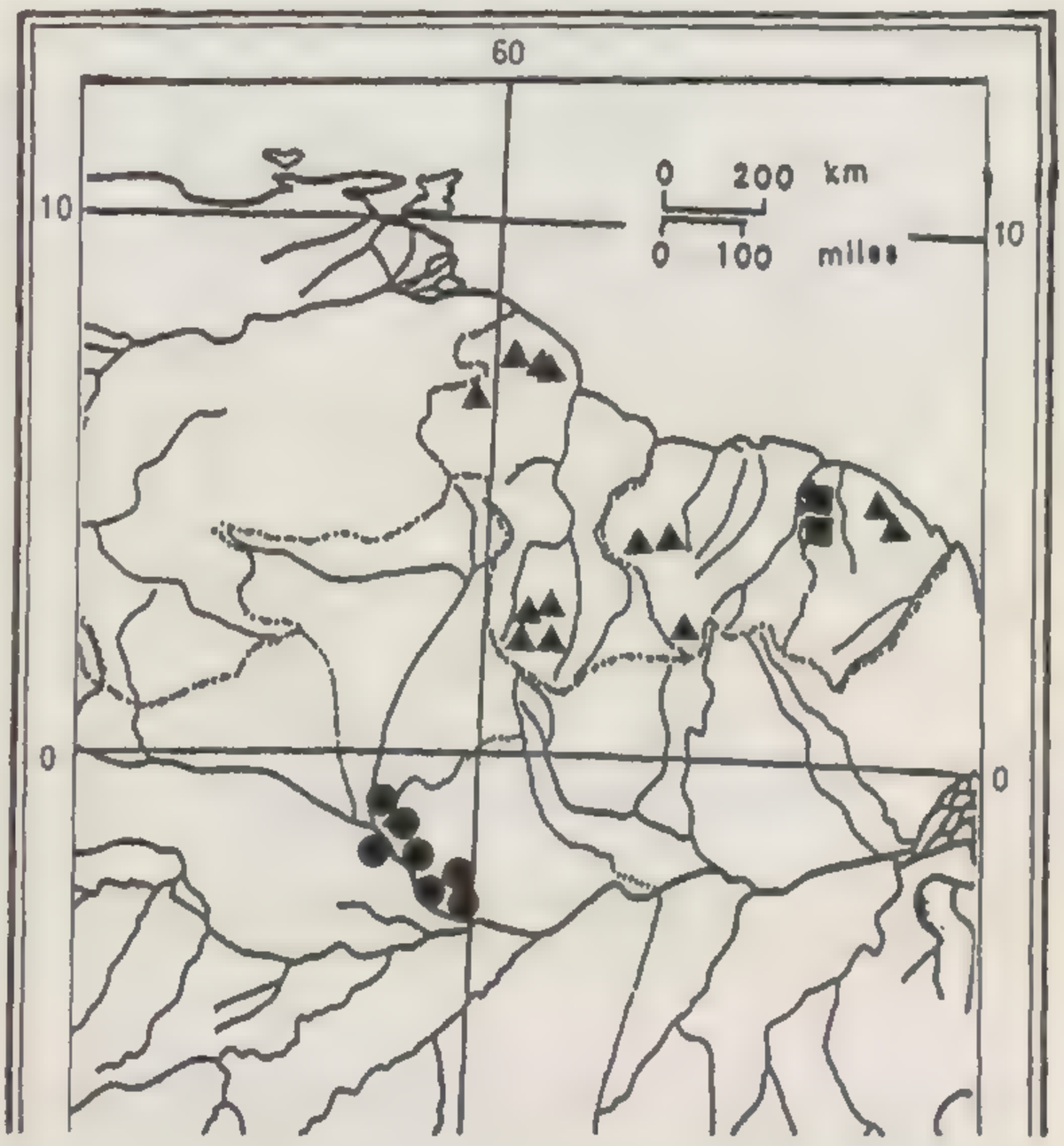


FIGURE 10. Distribution of *P. insignis* (circle), *P. macrostachya* (triangle), and *P. sulphurea* (square).

FIGURE 9. Distribution of *Petrea bracteata*.

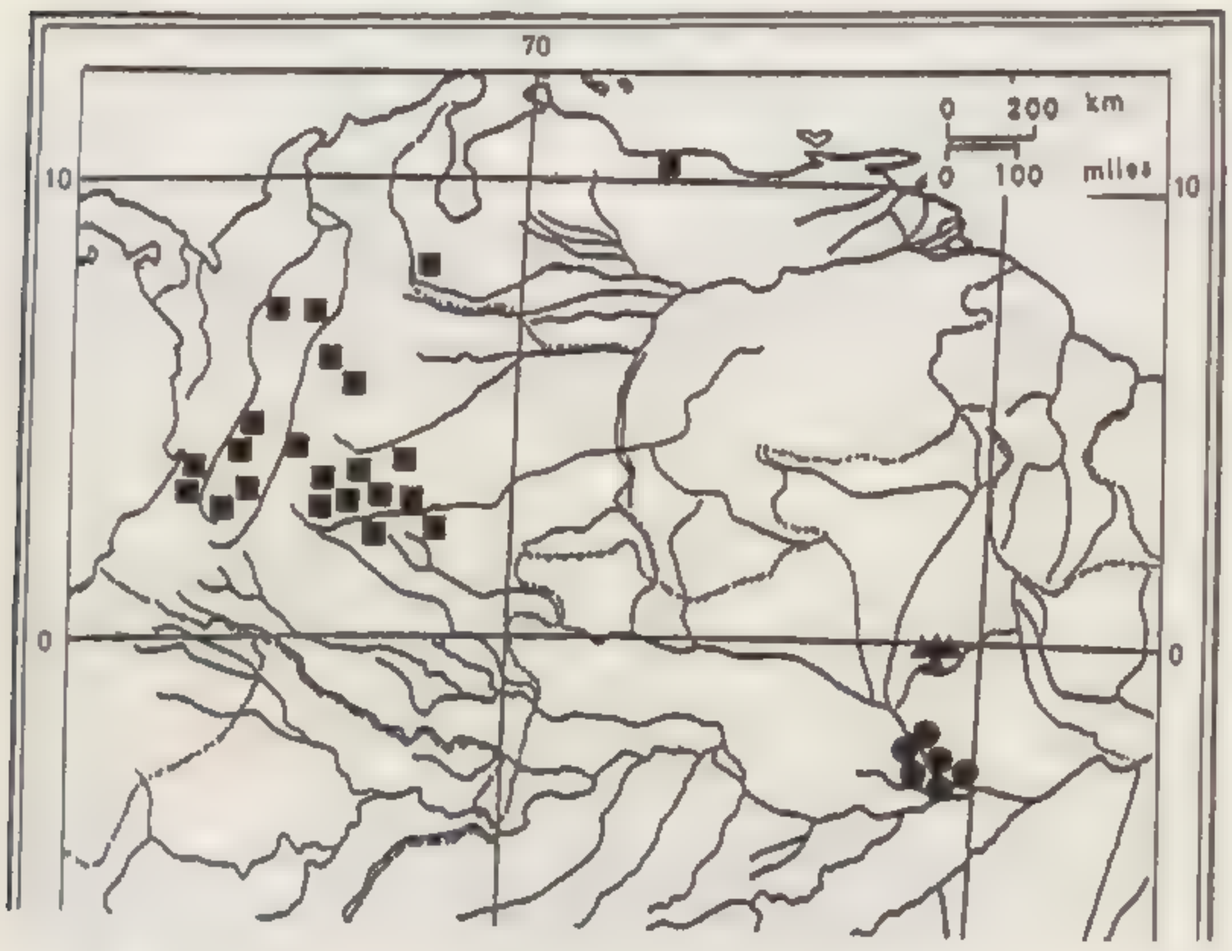


FIGURE 11. Distribution of *Petrea brevicalyx* (circle), *P. campinae* (triangle), and *P. rugosa* (square).

macrostachya, the species in the clade with pitted leaf beneath; (8) a clade formed by *P. brevicalyx* and *P. campinae*. The character shared among the last three species is the pitted leaves; *Petrea brevicalyx*, *P. campinae*, and *P. macrostachya* occur in northern Brazil and the Guianas, where the main concentration of species in the genus is found.

SYSTEMATIC TREATMENT

CRITERIA FOLLOWED IN THE SPECIFIC TREATMENTS

The delimitation of taxa was based on morphological characters that were measured as indicated in the Morphology section. Measurements of the leaves are given for mature leaves on terminal branches. For practical purposes, only discrete characters are included in the key. Moreover, only the characters that differ from those of the genus are given in the description of each species. A list of representative specimens examined is provided for each species. This list reflects as much as possible an overview of the distributional range as well

TABLE 4. Characters and character states for analysis of the tribe Petreeae.

0. Leaves smooth 0, rough-scabrous 1.
1. Leaf-scar swollen and corky 0, neither swollen nor corky 1.
2. Hairs not bulbous-based 0, hairs bulbous-based 1.
3. Calyx mainly dentate or truncate 0, calyx mainly lobed 1.
4. Degree of sepals fused: >0.50, 0; ≤0.50, 1.
5. Torus not swollen 0, swollen 1.
6. Calyx costate 0, not costate 1.
7. With staminode 0, without staminode 1.
8. Anthers sagittate 0, not sagittate 1.
9. Ovary without basal disk 0, with basal disk 1.

TABLE 5. Data matrix for the genera of the tribe Petreeae. The character states 0 = plesiomorphic, 1 = apomorphic. See Table 4 for definition of characters and character states.

Taxon	0	1	2	3	4	5	6	7	8	9
Citharexylum/ Duranta	0	0	0	0	0	0	0	0	0	0
Casselia	0	1	1	0	0	0	0	1	1	0
Lampaya	0	1	0	0	0	0	0	1	1	0
Petrea	1	0	1	1	1	1	1	0	1	1
Recordia	0	0	0	0	0	0	0	0	0	0
Xolocotzia	1	0	0	1	1	1	1	1	1	1

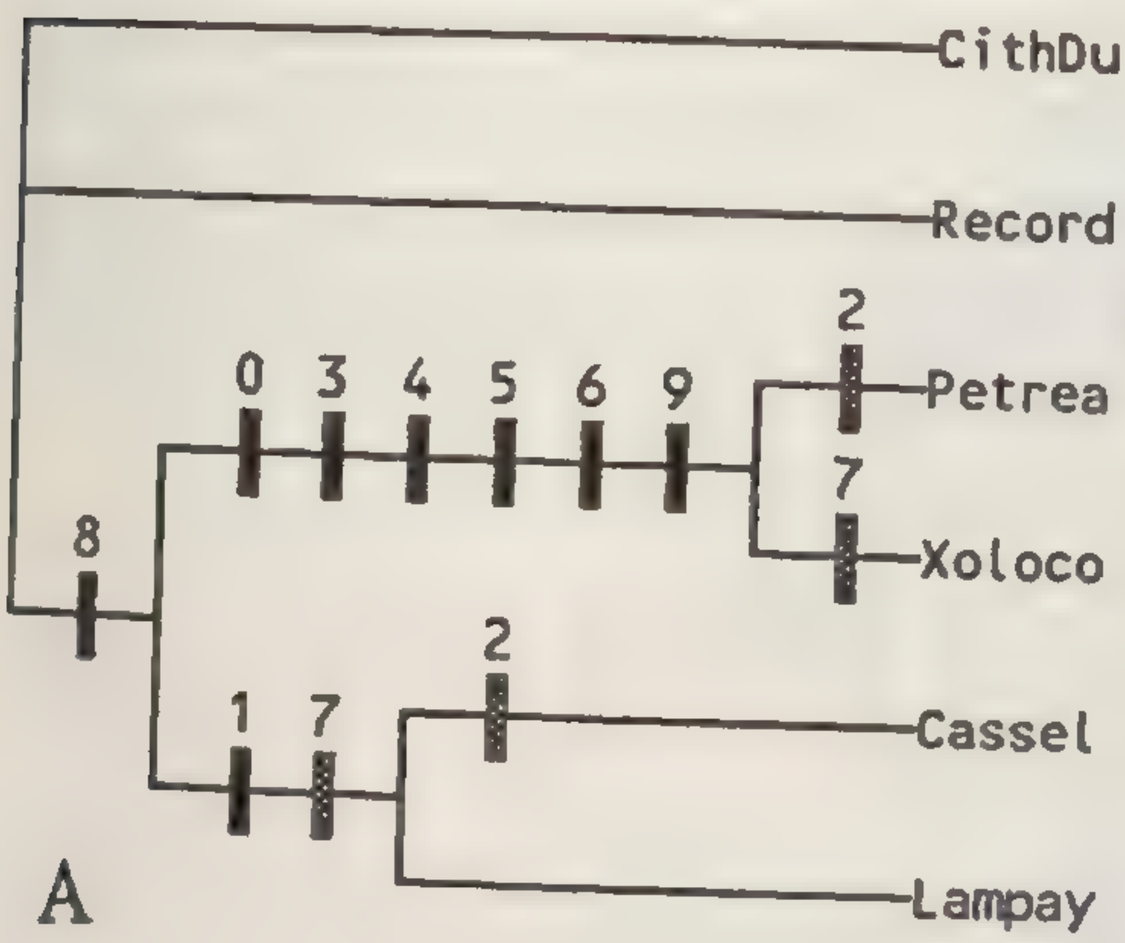
as collections represented in a large number of herbaria. However, on the maps provided for each species all of the collections examined have been plotted. All the specimens seen are listed in Appendix 1.

Petrea L., Sp. Pl., ed. 1: 626. 1753. TYPE: *P. volubilis* (LINN. 781.1).

Woody vines, shrubs, or trees. Leaves decussate-opposite or whorled, deciduous, often rough-

TABLE 6. Characters and character states for analysis of the genus *Petrea*.

0. Erect plants 0, climbers 1.
1. Longest petiole ≤10 mm 0, >10 mm 1.
2. Petioles without lateral traces 0, with two lateral traces 1, with four lateral traces 2.
3. Leaf apex rounded 0, cuspidate 1.
4. Leaves beneath smooth 0, bullate 1, pitted 2.
5. Epidermis with one row of cells 0, with more than one row 1.
6. Mesophyll with one layer of palisade tissue 0, with more than one layer 1.
7. Head of subsessile glandular hairs with >4 cells 0, <4 cells 1.
8. Clavate glandular hairs absent 0, present 1.
9. Stomata not in pits 0, in pits 1.
10. Stomata diallelocytic 0, anomocytic 1, paracytic 2.
11. Aborted axillary racemes absent 0, present 1.
12. Inflorescence terminal 0, axillary 1.
13. Longest floral pedicel length ≤ 15 mm 0, >15 mm 1.
14. Pedicel without a pair of bracteoles 0, with a pair of bracteoles 1.
15. Calyx pubescent 0, glabrous 1.
16. Calyx not corrugate 0, corrugate 1.
17. Calyx fusion ≤50% 0, >50% 1.
18. Calyx lobe axils separated 0, united 1.
19. Longest corolla tube ≤15 mm 0, >15 mm 1.
20. Ribbon hairs present in corolla 0, absent 1.
21. Staminode absent 0, present 1.
22. Style pubescent 0, glabrous 1.
23. Stigma subcapitate 0, capitate 1.



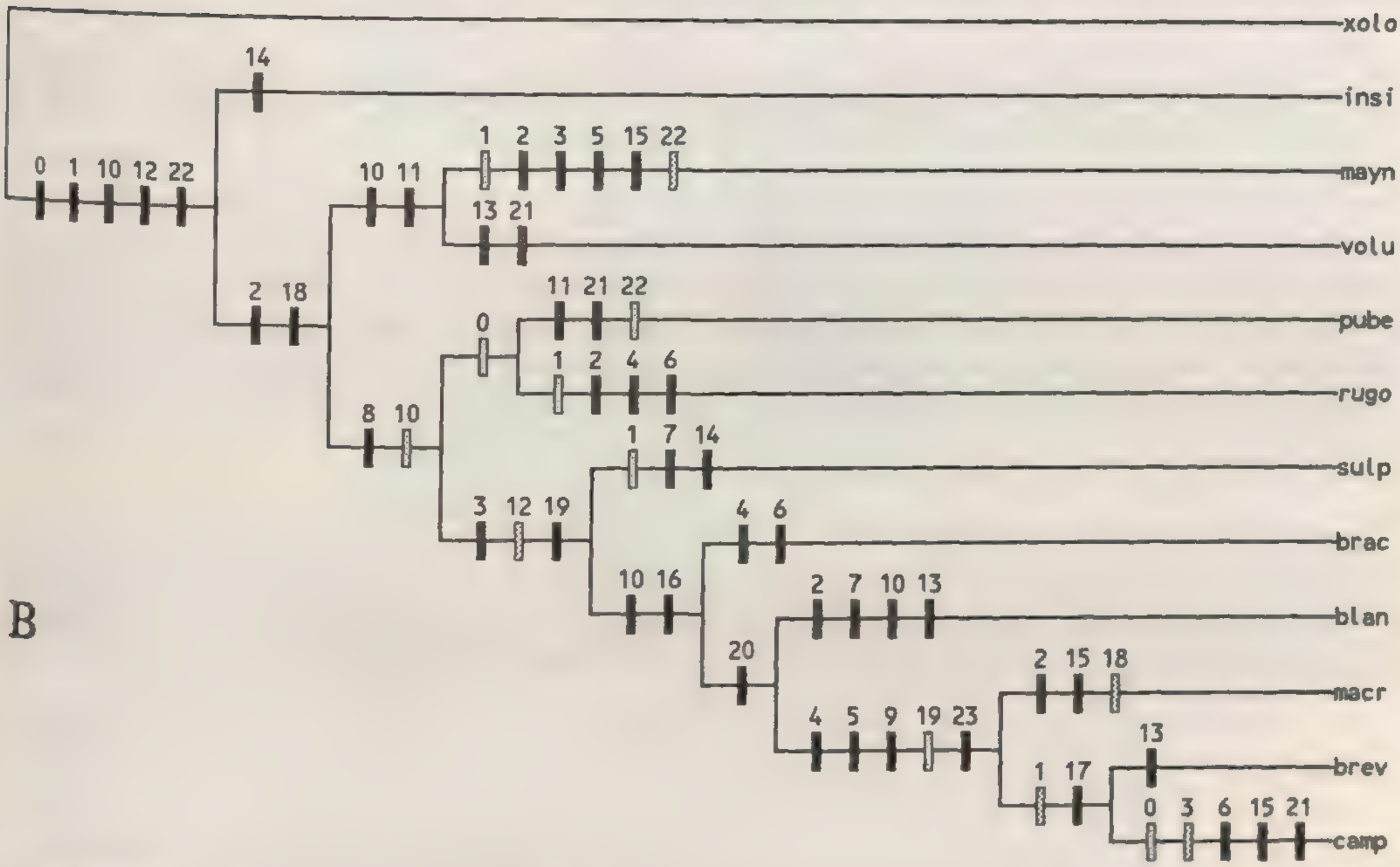


FIGURE 12. —A. Most parsimonious tree for relationships of the tribe *Petreeae*. —B. Most parsimonious tree for relationships of the species of the genus *Petrea*.

ened, brochidodromous. Inflorescence axillary or terminal, racemose, the rachis with several pairs of additional bractlets in the lower portion not subtending any flowers; bracts caducous. Flowers perfect, hypogynous, subtended by one or more bracteoles; torus mostly swollen; calyx gamosepalous, violet, purple, pale green, or white, mostly actinomorphic, the tube cylindric or campanulate, its rim normally 5-lobed, the lobes sometimes unequal, mostly longer than the tube, alternate with the petals; calycinal crest present in the inner part of the lobes, 5-lobed, the lobes alternate with the sepals; corolla gamopetalous, hypocrateriform, usually darker blue or purple than the calyx, sometimes white or yellow, occasionally with white or yellowish spot in the center, slightly zygomorphic, warty pubescent inside, the tube cylindric, urceolate, or infundibular, the limb rotate, normally 5-lobed, the lobes mostly of 2 sizes, much shorter than the calyx-lobes and alternate with them; stamens 4, didynamous, sometimes homodynamous, inserted near the middle of the corolla-tube, included; the filaments are wiry or stout flattened; anthers oblong or ovate, dorsifixed near the base, 2-celled, opening by longitudinal slits, introrse, the connective enlarged, often surpassing the thecae;

TABLE 7. Data matrix for the species of the genus *Petrea*. The character states 0 = plesiomorphic, 1 & 2 = apomorphic. See Table 6 for definitions of characters and character states and Table 3 for unabbreviated species epithets.

Taxa	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Xolo	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
blan	1	1	2	1	0	0	0	1	1	0	2	0	0	1	0	0	1	0	1	1	1	0	1	0
brac	1	1	1	1	1	0	1	0	1	0	1	0	0	0	0	0	1	0	1	1	0	0	1	0
brev	1	0	1	1	2	1	0	0	1	1	1	0	0	1	0	0	1	1	1	0	1	0	1	1
camp	0	0	1	0	2	1	1	0	1	1	1	0	0	0	0	1	1	1	1	0	1	1	1	1
insi	1	1	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	1	0
macr	1	1	2	1	2	1	0	0	1	1	1	0	0	0	0	1	1	0	0	0	1	0	1	1
mayn	1	0	2	1	0	1	0	0	0	0	2	1	1	0	0	1	0	0	1	0	0	0	0	0
pube	0	1	1	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	1	0	0	1	0	0
rugo	0	0	2	0	1	0	1	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0
sulp	1	0	1	1	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	1	0	0	1	0
volu	1	1	1	0	0	0	0	0	0	0	2	1	1	1	0	0	0	0	1	0	0	1	1	0

staminode sometimes present; basal nectariferous disk ca. 1 mm long and 2.5 mm wide; ovary superior, subglobose or oblong, borne on a conspicuous disk, 2-celled, each cell 1-ovulate, compound, but 1-carpellate through the abortion of one carpel; ovules lateral, ascending, hemianatropous, or orthotropous; style included in the corolla-tube, usually shorter than the stamens, single, terminal, filiform; stigma capitate, mostly oblique, bilobed. Fruit within the persistent calyx, the fruiting-calyx incrassate, its tube slightly accrescent, mostly losing its blue color, very hard, tough and usually ribbed, the lobes accrescent, reticulate-veined, divergent, the calycinal crest callose, curving inwards and converging, thus completely closing the mouth of the calyx-tube; fruit drupaceous, enclosed by the mature calyx, the exocarp leathery or fleshy, the endocarp hard, 2-celled, forming 2 stones, each stone 1-seeded, or by abortion the fruit 1-stoned and 1-seeded; seeds laterally or apically attached.

KEY TO THE LIVING SPECIES OF *PETREA*

1a. Inflorescence mainly axillary; leaf apex mostly rounded.
  2a. Pedicels with a pair of leaflike bracteoles; calyx lobe sinuses opened ..... 5. *P. insignis*
  2b. Pedicels without a pair of leaflike bracteoles; calyx lobe sinuses closed.
    3a. Climbing plants; clavate glandular hairs present.
      4a. Leaves ternate; the longest petiole ≤10 mm ..... 7. *P. maynensis*
      4b. Leaves opposite; the longest petiole >10 mm ..... 11. *P. volubilis*
    3b. Erect plants; clavate glandular hairs absent.
      5a. Tree with mature leaves not bullate; with aborted racemes; staminode present ..... 8. *P. pubescens*
      5b. Shrub with mature leaves bullate; without aborted racemes; staminode absent ..... 9. *P. rugosa*
1b. Inflorescence mainly terminal; leaf apex mostly cuspidate.
  6a. Calyx lobes of 2 sizes of lobes; corolla yellow; stem winged ..... 10. *P. sulphurea*
  6b. Calyx with equal-sized lobes; corolla blue; stem not winged.
    7a. Mature leaves bullate; mostly with three inflorescences at the tips of branches ..... 2. *P. bracteata*
    7b. Mature leaves smooth or pitted but not bullate; with one inflorescence at the tips of branches.
      8a. Mature leaves smooth, the stomata not in pits; the longest corolla tube >15 mm long ..... 1. *P. blanchetiana*
      8b. Mature leaves pitted, the stomata in pits; the longest corolla tube ≤15 mm long.
        9a. Longest petioles >10 mm; calyx not corrugate; calyx fusion ≤50%; calyx lobe sinuses opened ..... 6. *P. macrostachya*
        9b. Longest petioles ≤10 mm; calyx corrugate; calyx fusion >50%; calyx lobe sinuses closed.
          10a. Liana; the longest floral pedicel >15 mm; calyx pubescent ..... 3. *P. brevicalyx*
          10b. Shrub; the longest floral pedicels ≤15 mm; calyx glabrous ..... 4. *P. campinae*

1. Petrea blanchetiana Schauer in DC., Prod. 11: 617–618. 1847. TYPE: Brazil. Bahía: *Martius 1029* (lectotype, selected by Rueda (1993), BR; isolectotypes, BM, G(2), GH, L, LE, M(2), MO, NY, S; photo of isolectotype, NY). Figure 13.

FIGURE 13. Habit of *Petrea blanchetiana* Schauer (*Nevers 5812*).

Petrea peruviana Moldenke, Feddes Repert. 43: 206. 1938. TYPE: Peru. Loreto: Mishayacú, near Iquitos, 100 m elev., Dec. 1929 (fl, fr), *Klug 637* (holotype, NY; isotypes, F, US).

Petrea peruviana var. *acuminata* Feddes Repert. 43: 208. 1938. TYPE: Peru. Loreto: Iquitos, Jan. 1975, *Melin s.n.* (holotype, S; fragment of holotype, NY; photos of holotype and isotype, NY, TEX, US).

Petrea morii Moldenke, Phytologia 45: 469. 1980. TYPE: Panama. San Blas: El Llano Cartí road, 12 Apr. 1925, *Mori & Kallunki 5521* (holotype, US; isotype, MO; fruits of isotype and photo of holotype, TEX).

Petrea algentryi Moldenke, Phytologia 54: 67. 1983. TYPE: Colombia. Chocó: Río Tagachi, 12 km W of Río Atrato, 19 June 1982, *Gentry et al. 37075* (lectotype, selected by Rueda (1993), MO; isolectotype, MO).

Liana; the branchlets tetragonal, puberulent. Leaves with petioles 3–15 mm long, puberulent; blades ovate-elliptic, 6–30 cm long, 3–16 cm wide, the apex acute to acuminate, the base acute to subcordate, membranous, smooth to the touch or very slightly roughened, sometimes slightly pubescent on both surfaces, sometimes impressed-punctate on both surfaces. Inflorescences terminal, racemiform, 8–53 cm long, 3–9 cm wide; pedicels 10–31 mm long, often bearing a bracteole. Flowers with the calyx-tube 5–7 mm long, the base 2–3 mm wide, the apex 4–7 mm wide, corrugated, slightly pubescent, 5-lobed, the lobes membranous, obovate, 16–25 mm long, 2–4 mm wide at base, 5–9 mm wide at the widest point, the apex acute, glabrous; calycinal crest with the lobes ca. 1.5 mm long, 2 mm wide at base, the apex blunt, glabrous; corolla fragrant, 13–18 mm long, the base 1.5–2.5 mm wide, ampliate to 7–20(–50) mm across at apex, pubescent, the limb rotate, 5-lobed, the anterior lobe largest, the remaining lobes similar; stamens 4; filaments ca. 2 mm long, sparsely pilose; anthers ca. 1.5 mm long and 0.6 mm wide; ovary oblong, ca. 2 mm long and 1.5 mm wide, glabrous; style 2.5 mm long, glabrous; stigma subcapitate.

Distribution (Fig. 6). This species ranges from Panama to Venezuela, French Guiana, Brazil, and Peru. In Peru it is very common on white sand soils, growing up to 6 m in chamizal forest or up to 20 m on more fertile soil in varillal forest. It is sometimes found in patches; for example, Nevers (sub *3959*) reported seven individuals in full bloom growing within 150 m of each other in Panama.

Selected specimens examined. PANAMA. **San Blas:** El Llano–Cartí road, 24.5–25 km from Panamerican hwy., near continental divide, 12 Apr. 1975, *Mori & Kallunki 5521* (MO, TEX, US). COLOMBIA. **Vaupés:** Alto Vaupés, near Miraflores, 300 m, 2, 4, 5 Feb. 1944, *Gutiérrez & Schultes 760* (COL, GH, NY, S). VENEZUELA. **Amazonas:** Río Negro, 1–4 km E of Cerro Neblina, Camp on Río Mawarinuma, 140 m, 10 Feb. 1984, *Liesner & Funk 15826* (MO). FRENCH GUIANA. **Cayenne:** forest around the runway, 10 m, 10 Apr. 1983, *Kahn & Granville 5400* (BR, CAY(3), U); Creek Mulet Mort, S of Saul, 10 Feb. 1966, *Oldeman 2012* (CAY, TEX). PERU. **Amazonas:** Valle del Río de Santiago, Quebrada Caterpiza, 2–3 km behind Caterpiza community, 200 m, 29 Nov. 1979, *Tunqui 171* (MO, TEX). **Loreto:** Prov. Maynas, Tamshiyacu, 29 Nov. 1980, *Ayala et al. 2894* (F, MO, NY); Alpahuayo, 4 June 1986, *Ayala & Rimachi 4509* (MO); Via Nauta–Iquitos, 28 June 1979, *Díaz & Jaramillo 1243* (MO); Mishana, between Río Nanay and Río Itaya, 130 m, 29 Nov. 1977, *Gentry et al. 20982* (MO); Río Momón behind tourist camp, vicinity of Iquitos, 120 m, 12 May 1978, *Gentry et al. 21721* (F, MO(2), TEX); Iquitos, Mishuyacú, 100 m, Oct.–Nov. 1929, *Klug 170* (F, NY, US); Zungaro Cocha road, near Quebrada Shushuna, 160 m, 4 Feb. 1983, *Rimachi 6539* (BR, NY); Puerto Almendras, 7 July 1992, *Rueda & Ruiz 701* (MO); Fernando Lores, Tamshiyacu, Constancia, 50 m, 9 July 1992, *Rueda & Ruiz 730* (MO). BRAZIL. **Amazonas:** Amapá, Rio Oiapeque, Igarape Nataia 5 Feb. 1950, *Fróes 25871* (IAN, NY, S); São Paulo de Olivença, basin of Creek Belém, 26 Oct.–11 Dec. 1936 *Krukoff 9112* (NY). **Bahia:** 1857, *Blanchet s.n.* (BR(2)). **Distrito Federal:** Brasilia, *Blanch s.n.* (S); 1842, *Dupre s.n.* (P). **Pará:** 25 Sep. 1928, *Sampaio 5092* (NY, R). **Roraima:** Rio Maturuca, Missao Salesiana, 1 Jan. 1966, *Silva & Brazao 60806* (CAY).

Local names and uses. In Panama, "kwagi tupa"; Peru, "lija sacha," "lija caspi," "sanango sacha"; Venezuela, "tostadito." No use is known.

Petrea blanchetiana resembles *P. bracteata* but has smooth leaves and one inflorescence at the branch tip, as opposed to bullate leaves and mostly three inflorescences in *P. bracteata*. In addition, in the latter species the longest pedicels are less than 15 mm and in *P. blanchetiana* they are much longer than 15 mm. This species has the largest flowers known in the genus, up to 5 cm across when fresh.

2. Petrea bracteata Steudel, Flora 26: 764. 1843. TYPE: Suriname. Apr. 1842, *Hostmann & Kappler 39* (lectotype, selected by Rueda (1993), W; isolectotypes, B, BM, C, F, G(2), K, LE, MO, S, U, W(2); fragments of isolectotype, MO, NY; photos of isolectotype, MO, NY, TEX; photos of two isolectotypes overlaid in the same picture, NY). Figure 14.

Petrea martiana Schauer in DC., Prod. 11: 620. 1847. TYPE: Brazil. Pará: San Antonio de Gurupá, 3–16 Sep. 1819, *Martius s.n.* (lectotype, selected by Rueda (1993), M; fragment of lectotype, NY).

Petrea schomburgkiana Schauer in DC., Prod. 11: 619. 1847. TYPE: Guyana. 1840–1844, *Schomburgk 108* (photolectotype, selected by Rueda (1993), MO; duplicate photos, TEX, US).

Petrea martiana var. *glabrescens* Moldenke, Phytologia 32: 458. 1975. TYPE: Brazil. Pará: Curucambám, Obidos, 9 June 1926, *Ducke 14291* (holotype, NY).

FIGURE 14. *Petrea bracteata* Steudel (*Feuillet 739*).—A. Habit.—B. Flower.

Liana; the branchlets tetragonal, short-pubescent; often with one or two leaflike bracts below the petioles or on the outer side of the branchlets. Leaves with petioles 5–20 mm long, short-pubescent; blades ovate-elliptic, 3.5–30 cm long, 1.8–13.5 cm wide, the apex obtusely acute or very short-acuminate, the base acute to broadly rounded, membranous or subcoriaceous, very densely asperous on both surfaces, bullate beneath when mature. Inflorescences mainly terminal, racemiform, 19–50 cm long, 4–9 cm wide; pedicels to 1 cm long; puberulent. Flowers with the calyx-tube

4–5 mm long, the base ca. 3 mm wide, 4–5.5 mm wide at apex, corrugated, short-pubescent, 5-lobed, the lobes membranous, oblong or elliptic, 11.5–17 mm long, the base 2–3 mm wide, the widest point 3–10 mm wide, the apex rounded or acute, glabrous; calycinal crest with the lobes ca. 1.5 mm long, 1 mm wide at the base, the apex blunt, glabrous; corolla with throat white and hairy, 8.5–20 mm long, the base 2–3 mm wide, ampliate to 6.5–9 mm at the apex, pubescent, the limb rotate, 5-lobed, the anterior lobe larger, the remaining lobes similar; stamens 4; filaments ca. 2 mm long, sparsely pilose; anthers ca. 2 mm long; ovary obovate, ca. 2 mm long and wide, glabrous; style ca. 2.5 mm long, glabrous; stigma subcapitate.

Distribution (Fig. 9). This species is found from Venezuela and the Guianas to Brazil and Peru.

Selected specimens examined. VENEZUELA. **Amazonas:** Río Orinoco, between Tama-Tama and Caño Manaviche, 150 m, 19 Apr. 1954, *Level 5* (NY); Río Cunucunuma, 30 km from Playa Alta, 200 m, 28 Dec. 1950, *Maguire et al. 30444* (NY, S, US). GUYANA. Groete Creek, 10 Oct. 1948, *Atkinson 4* (BM, MICH); Essequibo Islands, Bartica, on bank of Essequibo river, 5 Nov. 1948, *Atkinson 17* (BM); Mazaruni–Potaro, junction of Mazaruni and Cuyuni rivers, July 1914, *Graham 254* (NY, US); St. Elie road, 4 Mar. 1978, *Raynal-Roques 20183* (CAY). SURINAME. Brokopondo, along trail from Brownsweg to Mazaroni peak, 300 m, 11 Feb. 1963, *Boer 642* (BR, U); Brokopondo natural reserve, Brownsberg small fall above Mazaroni fall, 15 Mar. 1976, *Tjon-Lim-Sang & Wiel 188* (U); Marowijne, Nassua mountains, Marowijne river, 475 m, 10 Jan. 1955, *Cowan & Lindeman 39221* (B, NY, S, U); Bakhuis-mountains, SW slopes, 818 m, 4 Mar. 1966, *Florschutz & Maas 3145* (U). FRENCH GUIANA. **Cayenne:** road St. Laurent to Paul Isnard, 15 Nov. 1982, *Billiet & Jadin 1697* (BR, CAY, U); Sinnamary River, 25 Feb. 1988, *Billiet & Jadin 4481* (BR, CAY); 20 km of Petit Saut road, 40 m, 26 Feb. 1988, *Billiet & Jadin 4510* (BR, CAY); S of St. Jean du Maroni, 19 Feb. 1956, *Cremers 7673* (CAY); region of Paul Isnard, Mont du Decou Decou, 400 m, 8 Sep. 1983, *Cremers 8175* (CAY, U); Piste de Saint-Elie, 22 Apr. 1984, *Sauvain 119* (CAY(3), U). PERU. **Cerro de Pasco:** Oxapampa, Palcazú Valley, Iscozacin, above PEPP project camp; forestry experimental strip, 6 Apr. 1985, *Salick 7251* (MO). **Loreto:** Maynas, Explornapo Camp, Quebrada Sucusari, N side, tributary of Río Napo, 140 m, 14 June 1986, *Gentry et al. 54345* (MO); road Nauta–Iquitos, 3 km N of Nauta, 140 m, 28 June 1979, *Díaz & Jaramillo 1243* (MO); Mishana, trail from village to Campamento 1, 140 m, 22 July 1980, *Gentry et al. 28928* (TEX); Río Santa María, trail E of Sencoya, 100 m, 9 Feb. 1979, *King 493* (F); Nauta, Quebrada Sapira, near Florida, ca. 8 km above Nauta, 26 May 1979, *McDaniel 22533* (F, BR); Explorama forest in the tourist camp of Explorama, 110 m, 30 June 1992, *Rueda & Ruiz 590* (MO); forest of the Research Institute of Peruvian Amazon, km 21 on road Quistococha–Nauta, 5 July 1992, *Rueda & Ruiz 628* (MO); Tahuampa forest around the town of Manacamiri, 6 July 1992, *Rueda & Ruiz 681* (MO); Fernando Lores, Tamshiyacu, Constancia, 50 m, 9 July 1992, *Rueda & Ruiz 720* (MO); Requena, 4 km NE of Arboretum Jenaro Herrera, along Río Ucayalí, Quebrada de Colima, 180 m, 13 Nov. 1981, *Spichiger & Encarnación 1039* (G(4), MO, NY); Bora native community of Brillo Nuevo, ca. 150 km of Yaguasyacu river, 106 m, 13 Nov. 1981, *Treacy & Alcorn 519* (F). **San Martin:** Lamas, Convento, trail to Tiyacu and Nuevo Lamas, km 68 of Tarapoto–Yurinawas road, 200 m, 19 Apr. 1986, *Knapp & Mallet 7120* (F). BRAZIL. **Amazonas:** km 148, on Manaus–Caracaraí road, 24 Sep. 1973, *Bisby et al. P18063* (NY); Uaupes, San Gabriel de Cachoeira, 19 Feb. 1975, *Cordeiro 220* (IAN); Esperanza, Rio Javarí, 3 Feb. 1942, *Ducke 872* (F, IAN, MO, R); Manaus, Ducke reserve, 23 Jan. 1963, *Lanna & Castellano 338* (TEX); Rio Javarí, 8 Aug. 1973, *Lleras et al. P17213* (INPA, NY); Manaus, between Boa Vista road and Itacoatiara road, ca. 60 km N of Manaus, 17 Apr. 1981, *Lowe 4087* (INPA); Rio Negro, between Manaus and São Gabriel along BR 307, São Gabriel, near Igarape Freitas and at Equator, 17 July 1979, *Poole 2021* (INPA, MG, NY); Manaus–Igarape, 5 km from Manaus–Caracaraí road, 26 Jan. 1971, *Prance et al. 11454* (NY, TEX); Cachoeira Republica, Rio Curuquete, 25 July 1971, *Prance et al. 14620* (F, NY, S, TEX); Rio Negro, road from Camanaus to Uaupes airport, 30 Oct. 1971, *Prance 15858* (INPA, NY, S, TEX, US); base of Serra Araca, 0–3 km S of Central Masiff, 3 km E of Rio Javarí, 8 Feb. 1984, *Prance et al. 28906* (NY); Totobi, basin of Río Demeni, 25 Feb. 1969, *Prance 10236* (F, MG, NY, R, S); Manaus–Caracaraí road, km 45, Campina reserve, 11 Dec. 1980, *Renner 57* (INPA, TEX, US); Rio Negro São Gabriel, 19 Feb. 1975, *Ribeiro s.n.* (TEX, S); Igarape da Cachoira Alta do Taruma, 28 Dec. 1961, *Rodrigues & Chagas 4041* (NY). **Mato Grosso Norte:** Jatuarana river, Machado river region, Dec. 1931, *Krukoff 1575* (BM, G, GH, S, U). **Pará:** Oriximina, left margin of Rio Mapuera, 3 Aug. 1985, *Almeida 213* (MG); left margin of Cachoeira Vira-Mondo, 5 Aug. 1985, *Almeida 229* (MG); Rio Trombetas km 54, access road from Cachoeira Porteira to Perimetral do Norte, 24 May 1974, *Campbell et al. P22257* (NY, TEX, US); basin of Rio Trombetas, 3 km S of Cachoeira Porteira, 8 June 1974, *Campbell et al. P22570* (M, MG, MO, NY); Oriximina, Rio Trombetas, left margin across Mineraçao Santa Patricia, 13 June 1980, *Cid et al. 1481* (INPA); Rio Branco de Obidos, 11 Dec. 1913, *Ducke 15127* (BM(2), G); Rio Negro, Alto Padauiry, 19 Oct. 1947, *Froes 22628* (IAN, NY); Estrada BR-163, near Rio Cuminamirin, 74 km of Oriximina, 60 m 3 Apr. 1980, *Martinelli 6757* (INPA, NY); BR 163, km 1229; Cuiaba–Santarem hwy., 18 Nov. 1977, *Prance et al. P25519* (F, GH, HBG, MG, MO). **Rondônia:** basin of Rio Madeira, 8 km NE of Porto Velho, 7 Nov. 1968, *Prance et al. 8256* (F(2), MG, NY, S, TEX); Cuiaba–Santarem, km 1180, 17 Nov. 1977, *Silva et al. 240* (MG, NY, U); Tapajó National Park, Villa Pimental, 25 Nov. 1978, *Silva & Rosario 3939* (MG, NY).

Local names and uses. In Brazil "viuvinha"; Guyana, "sandpaper"; Peru, "ana yo ki," "hierba aspera"; Suriname, "batjetje." In Peru its leaves are used to clean out guns; also the leaves are soaked in water until the liquid is black and then applied to snakebites (*Salick 7251*).

The presence of bullate mature leaves (see Fig. 14B) in *P. bracteata* makes this species easy to separate from the closely related species *P. blanchetiana* (see discussion under the latter species).

3. **Petrea brevicalyx** Ducke, Bull. Mus. Hist. Nat. Paris, ser. 2, 4: 748–749. 1932. TYPE: Brazil. Amazonas: Manaus, Igarapé da Cachoeira Grande, at the borders of swamps and on river shores, *Ducke s.n.* (lectotype, selected by Rueda (1993), NY; isolectotypes, G, K, RB, S, U, US; photos of isolectotypes, GH(2), NY, TEX). Figure 15.

Liana; the branchlets tetragonal or subterete, with minutely glandular-based hairs. Leaves with petioles 0.5–3 cm long, short-pubescent; blades elliptic or obovate-oblong, 5–16 cm long, 3–9 cm wide, the apex obtuse, the base acute or attenuate, coriaceous, rough to the touch, minutely pubescent above, intricately pitted beneath with abundant short hairs in the pits. Inflorescences mainly terminal, racemiform, 12–55 cm long, 2–3.5 cm wide; pedicels 0.5–2 cm long, minutely pubescent; bracts caducous. Flowers with the calyx-tube 6–10 mm long, corrugated, minutely puberulent, 5-lobed, the lobes membranous, triangular-ovate, 2–3 mm long; calycinal crest with the lobes ca. 1 mm long, the apex truncate; corolla deep violet, glandular short pubescent, 8–15 mm long, one of the lobes slightly longer than the others; stamens 4; the filaments ca. 1.5 mm long, sparsely pilose; anthers oblong; ovary oblong; style ca. 2.5 mm long, glabrous; stigma capitate, bilobed.

Distribution (Fig. 11). This species is only known from Brazil (Amazonas), growing in igapó (black-water inundated forest) on sandy river banks.

Specimens examined. BRAZIL. **Amazonas:** Manaus, Estrado do Francês Novo, 31 Jan. 1959, *Chagas 39* (MG, UB); Igarapé da Cachoeira Grande, 7 Dec. 1927, *Ducke s.n.* (K, G, NY, S, U, US), 29 Jan. 1936, *Ducke 110* (F, GH, IAN, MO, NY, UC, US), 22 Feb. 1945, *Fróes 20501* (IAN, NY, US); ZF3, BR 174, Fazenda Porto Alegre, 20 Mar. 1986, *Garcia 18* (MG), Nov. 1918, *Kuhlmann 2276* (NY, SP); road Manaus to Manacapuru, km 35, 5 Jan. 1967, *Prance et al. 3912* (F, INPA, NY, S); Rio Negro, Dec. 1901, *Ule 5982* (G, NY).

Local names and uses. In Brazil "cipó de fogo," "viuvinha." No use is known. It is most closely related to *P. campinae* (see discussion under that species).

4. **Petrea campinae** Rueda, Novon 4: 417. 1992. TYPE: Brazil. Roraima: along the road from Manaus to Caracaraí, km 350, left side, 00°06′N, 60°40′W, 12 Feb. 1979 (fl), *Rodrigues et al. 10100* (holotype, MG; isotypes, COL, INPA; drawing of holotype, MO). Figure 16.

Shrub 1.5–5 m tall; the branchlets tetragonal or subterete, minutely pubescent, pith well developed. Leaves with petiole 3–8 mm long; blades elliptic, 5–10 cm long, 1.5–6 cm wide, the apex apiculate or truncate, the base obtuse, coriaceous, asperous, glabrous above, intricately pitted beneath with abundant short hairs in the pits. Inflorescences mainly terminal, racemiform, 10–22 cm long, 2–5 cm wide; bracts setaceous to foliaceous; pedicels 6–10 mm long, pubescent. Flowers with calyx corrugate, glabrous, 5-lobed, unequal, rounded, 4–8 mm long; calycinal crest with the lobes ca. 1.5 mm long; corolla 1.2–1.5 cm long, the limb lobed, 5–8 mm wide, the lobes 5, ovate, 3–6 mm long, unequal; straight or curved, blue, glandular-pubescent; stamens 4, the filaments ca. 1.5 mm long, the anthers oblong, staminode sometimes present; ovary globose, the style 2–3 mm long, glabrous; the stigma capitate.

Distribution (Fig. 11). This species is only known from a few patches of scrub campina forest on white sand, near km 350 on the Manaus–Caracaraí road, in Roraima, Brazil.

Specimens examined. BRAZIL. Roraima: along BR 174, between Manaus and Caracaraí, 6 km S of equator, in a campina, 00°04′S 60°40′W, 17 June 1985, *Cordeiro et al. 76* (INPA, SP).

Local names and uses. None reported.

Petrea campinae resembles *P. brevicalyx* in having elliptic leaves that are intricately pitted beneath and a calyx with short rounded lobes. It differs in its erect habit and its unequal calyx lobes twice as long as those of the lianaceous *P. brevicalyx*.

5. **Petrea insignis** Schauer, in DC., Prod. 11: 620. 1847. TYPE: Brazil. Pará: exact locality unknown, 1–21 Aug. 1819, *Martius s.n.* (holotype, M). Figure 17.

Petrea duckei Moldenke, Phytologia 1: 469–470. 1940. TYPE: Brazil. Amazonas: lower Rio Negro, Paraná de Anavilhana, on inundated shores, 24 July 1929, *Ducke s.n.* (holotype, NY; isotype, RB).

Liana; the branchlets puberulent-asperulous. Leaves with petiole 3.5–12 mm long, with minute dark brown hairs; blades elliptic, 3–18.5 cm long, 1.5–8 cm wide, the apex acute or obtuse, the base

FIGURE 15. Habit of *Petrea brevicalyx* Ducke (*Fróes 20501*).

acute or rounded, chartaceous; membranous, somewhat asperous, glossy and glandular above, glabrous beneath except on the minutely pubescent veins. Inflorescences axillary, racemiform, 14–37 cm long; bracts elliptic, apiculate, 6–10 mm long, bractlets leaflike, in pairs on the pedicels; pedicels 3–15 mm long, glandular-puberulent. Flowers with calyx-tube 5–10 mm long, 5-lobed, the lobes petaloid, sinuses between petals opened, obovate, 10-13 mm long, 12 mm wide, puberulent; calycinal crest with the lobes ca. 5 mm long; corolla 12–16 mm long, the limb 5-lobed, one of the lobes slightly

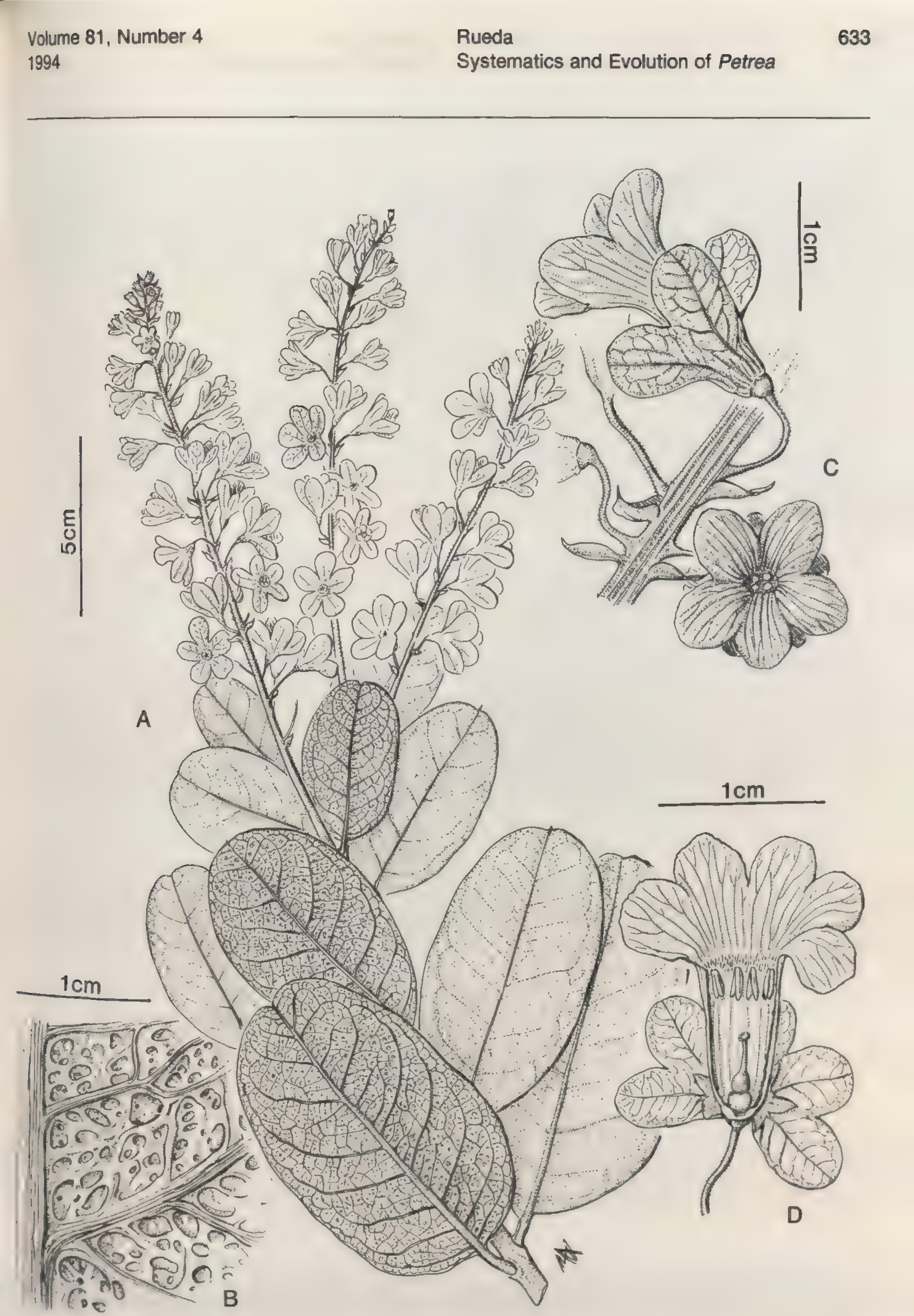


FIGURE 16. *Petrea campinae* Rueda (*Rodrigues et al. 10100*).—A. Habit.—B. Close up of abaxial leaf surface, showing pits.—C. Flower.—D. Flower, cut longitudinally and laid open.

FIGURE 17. Habit of *Petrea insignis* Schauer (*Anderson 229*).

larger than the others, short-pubescent; stamens 4, filaments ca. 2 mm long, anthers oblong; ovary oblong, the style ca. 3 mm long, glabrous; stigma subcapitate.

Distribution (Fig. 10). This species is endemic to Brazil (Amazonas), growing on white sand river banks, along black-water-flooded rivers.

Selected specimens examined. BRAZIL. **Amazonas:** Manaus, Francês Novo, 12 Mar. 1956, *Chagas s.n.* (TEX); Barcelos, margins of Rio Aracá, 29 July 1985, *Cordeiro 307* (SP); Rio Taruma, 14 Aug. 1949, *Fróes 25053* (NY(2)); Igarapé Ponta Negra, 22 May 1955, *Frões 29568* (IAN); Rio Negro opposite Manaus, 3-6 km upstream, 8 Apr. 1971, *Prance et al. 11768* (NY, TEX, U), 21 June 1882, *Schwacke 3638* (G); Rio Negro, river side and small islets of Rio Negro within 100 km upstream from Manaus, 13 Aug. 1987, *Tsugaru & Sano B-1001* (NY).

Local names and uses. In Brazil "flor de Saõ Miguel," "viuvinha." No uses have been recorded.

This species is quite distinct and is the sister group to the rest of the genus in the cladistic analysis, thus appearing to be a relict. However, it shares some characters with more advanced species, such as bractlets on the petioles as in *P. sulphurea* and calyx hole sinuses opened as in *P. macrostachya*, but neither of these species has a terminal inflorescence or the leaf apex cuspidate as in *P. insignis*. Whereas the wide geographic distribution of *P. volubilis* has been perceived as supporting its primitive position in the genus, this is not supported by the cladistic analysis. Perhaps this greater distribution of *P. volubilis* is a result of increased dispersability of the lighter calyx.

6. **Petrea macrostachya** Bentham, Ann. Nat. Hist., ser. 1, 2: 448. 1839. TYPE: Guyana. Along the brook Currapawaak, 1835–1839, *Schomburgk 158* (lectotype, selected by Rueda (1993), K; isolectotypes, BM, BR, F, G, GH, K(2), LE; fragment of isolectotype, NY; photos of isolectotypes, F, MO, TEX). Figure 18.

Liana; the branchlets obtusely tetragonal, minutely pubescent. Leaves with petioles 4–20 mm long, minutely puberulent; blades broadly elliptic or ovate-elliptic, 5–21 cm long, 2.5–15 cm wide, the apex obtuse or acuminate, sometimes apiculate, the base rounded or acute, coriaceous, asperous, glabrous above, intricately pitted beneath with abundant short hairs in the pits, with strongly defined veinlets delimiting the pits. Inflorescences mainly terminal, racemiform, many-flowered, 20–70 cm long; bracts 2–8 mm long; pedicels 4–15 mm long, minutely puberulent. Flowers with the calyx-tube 6–11 mm long, glabrous, 5-lobed, the lobes obovate, 15–35 mm long, 3–10 mm wide, with the sinuses between petals opened; calycinal crest with lobes ca. 1 mm long, the apex obtuse or rounded, glabrous; corolla blue to violet-purple, 8–13 mm long, the lobes 5–12 mm long, one larger than the other 4, the apex rounded, short pubescent; stamens 4; the filaments ca. 2 mm long, the anthers ca. 1 mm long; ovary oblong, 1–2 mm long, glabrous; style ca. 2.5 mm long, glabrous; stigma capitate.

Distribution (Fig. 10). *Petrea macrostachya* is endemic to Guyana, French Guiana, and Suriname, growing in high dense forest, along creeks, savanna edges, in forest of *Eperua* and *Mora* on sand, and in swampy forest. It is common in these habitats, climbing up to 10 m or more in crowns of *Diplotropis* and *Mora* trees, at altitudes up to 800 m.

Selected specimens examined. GUYANA. Mazuruni river, Takutu Creek to Puruni river, 29 Nov. 1944, *Forest Department of Guyana 4854* (NY); Potaro–Siparuni region, approximately 1–3 km SW of Paramakatoi, 650 m, 13 Mar. 1989, *Hahn et al. 5644* (US); Kanuku mountains, along creek, 300 m, 21 Feb. 1985, *Jansen-Jacobs et al. 341* (B, CAY, MO, WIS); upper Demerara region, Mabura hill, 150 m, 16 Sep. 1986, *Pipoly & Boyan 8517* (US); along the brook Currapawaak, 1835–1839, *Schomburgk 158* (BM, BR(2), F, G, GH, K(2), NY); basin of Kuyuwini river (Essequibo tributary), ca. 150 mi. from mouth, 21–26 Nov. 1937, *Smith 2626* (F, G, GH, MAD, U). SURINAME. 9 km N of Lucie river, 12 km W of Oost River, 275 m, 31 July 1963, *Irwin et al. 54511* (F, NY); Sipaliwini savanna area on Brazilian frontier, 3–5 km NW of Meyers farm, at hill foot toward river valley, Feb. 1970, *Oldenburger et al. 1261* (U); Wihelmina mountains, creek valley at the S base of Juliana Top, 5 Aug. 1963, *Schultz 10330* (U, US, WIS). FRENCH GUIANA. Cayenne, E road in the mountains near Neyrat, 4 Feb. 1977, *Cremers 4302* (CAY); on Kourou road near Montsinery road, 18 Apr. 1982, *Fournet 201* (CAY).

Local names and uses. It is called "sandpaper vine" in Guyana. No use is known.

This species is closely related to *P. brevicalyx* and *P. campinae*, which also have pitted leaves. However, *P. macrostachya* is the only species among the three that has the calyx united less than half of the total length and the calyx lobe sinuses opened. This species has the longest rachis in the genus (reportedly to 70 cm, presumably the source of the specific epithet).

7. **Petrea maynensis** Huber, Bol. Mus. Pará., 4: 602. 1906. TYPE: Peru. Loreto: Río Ucayalí, between Contamana and Canchahuaya, Nov. 1898, *Huber 1489* (lectotype, selected by Rueda (1993), MG; isolectotype, RB; fragment of lectotype, F; photo of lectotype, F, NY, TEX). Figure 19.

Petrea longifolia Moldenke, Feddes Repert. 43: 197. 1938. TYPE: without locality, date, or collector (holotype, P; isotype, P; fragments of holotype, F, NY; photos of holotype, NY, TEX).

Liana; the branchlets obtusely tetragonal, often striate-costate, short-pubescent. Leaves whorled in 3s or 4s, rarely some decussate-opposite; petioles 5–11 mm long, puberulent; blades elliptic or ovate, 5–32 cm long, 2–9 cm wide, the apex acute or obtuse, the base acute, slightly asperulous on both surfaces. Inflorescences axillary, the racemes 6–50 cm long, 2.5–5 cm wide, with aborted racemes in its axils; pedicels 4–9 mm long. Flowers with the calyx-tube 3–5 mm long, 2–4 mm wide at the base, ca. 5 mm wide at apex, glabrous, 5-lobed, the lobes membranous, oblong, 11–15 mm long,

3.0 cm
P. BICK

FIGURE 19. Habit of *Petrea maynensis* Huber (*Ferreyra 8100*).

←

FIGURE 18. Habit of *Petrea macrostachya* Benth. (*Schulz 10330*).

2–4 mm wide, the apex acute, glabrous; calycinal crest with the lobes ca. 2.5 mm long, and ca. 1 mm wide, the apex acute, glabrous; corolla fragrant, with white spots at throat, corolla-tube ca. 8 mm long, the base ca. 2.5 mm wide, to ca. 6 mm at apex, short-pubescent, the limb sometimes with dark blue lines, rotate, 5-parted, the anterior lobe largest, and sometimes white with blue margins, the remaining lobes similar, smaller, and light blue; stamens 4; filaments ca. 1.5 mm long, glabrous; anthers ca. 1 mm long and ca. 0.5 mm wide, the connective ending with an erect apiculation, glabrous; ovary oblong, ca. 1.5 mm long and ca. 1 mm wide, short-pubescent; style ca. 2 mm long, short-pubescent; stigma subcapitate, bilobed.

Distribution (Fig. 7). This species occurs from Colombia through Ecuador, Brazil, Peru, and Bolivia, growing on non-alluvial red clay soil, on river banks, and forested hills in tropical rainforest and in flood plain forest (varzea). It has been reported from altitudes from 100 to 750 m, sometimes occurring in forest characterized by scattered huge emergent trees of *Bertholletia exelsa* Humboldt & Bonpland.

Selected specimens examined. COLOMBIA. **Cundinamarca:** Medina, along left margin of Río Humea, 450 m, 4 Mar. 1987, *Lozano 5426* (COL). **Meta:** La Macarena, S side of Río Guayabero, 14 Mar. 1959, *Barclay 7146* (MO). **Vaupés:** near Miraflores, 300 m, 8, 10, 14 Feb. 1914, *Gutiérrez & Schultes 783* (COL, GH). ECUADOR. **Morona–Santiago:** Gualaquiza, Misión Bomboiza, 750 m, 27 Sep.–4 Oct. 1967, *Sparre 19187* (UEC). **Napo:** Río Napo & Río Huabuno junction, 450 m, 11 June 1985, *Marles EE80* (F, MO); Jatun Sacha reserve, trails 1 and 3, near Río Chinguipino, 380 m, 11 Aug. 1992, *Rueda 1128* (MO); Reserva de Producción Faunistica Cuyabeno, 1 km N of Laguna Grande, trail behind the Cuyabeno Station, Apr.–Oct. 1988, *Paz y Miño 81.012* (MO). PERU. **Amazonas:** Río Cenepa, Huampami, ca. 5 km E of Quebrada Chigki Shinuk, 200 m, 11 Aug. 1978, *Ancuash 1388* (F, MO, TEX); Río Santiago, 180 m, 14 Nov. 1979, *Tunqui 53* (MO, TEX(2)). **Huanuco:** near Puente Tulumayo, road Tingo Maria Pucallpa, 700 m, 2 Oct. 1950, *Ferreyra 8100* (MO, US); Pachitea, Honoria forest in San Marcos, Turnavista, 350 m, 1 Aug. 1968, *Schunke 2131* (F, G, NY, US). **Loreto:** Yurimaguas, road to Tarapoto, 150 m, 15 Sep. 1948, *Ferreyra 4496A* (MO); Fernando Lores, Tamshiyacu, trails between Constancia and Serafin, 50 m, 10 July 1992, *Rueda & Ruiz 808* (MO). **Madre de Dios:** Tambopata, Río Tambopata reserve, at mouth of Río D'Orbingy, 250 m, 2 Mar. 1981, *Gentry & Young 31877* (MO, TEX); Manu National Park, Cocha Cashú uplands, 400 m, 11 Sep. 1986, *Nuñez 6083* (MO). **San Martin:** Tocache Nuevo, SE of Tocache Nuevo airport, 400 m, 19 Jan. 1970, *Schunke 3682* (F, G, NY, US). BRAZIL. **Acre:** Canamari, downstream from Cruziero do Sul, 150 m, 23 Aug. 1986, *Croat 62570* (MO); 12 km from Rio Branco, on Rio Branco–Porto Velho road, 30 Sep. 1980, *Lowrie et al. 291* (GH, MG, MO, NY). **Amazonas:** São Paulo de Olivença, Rio Solimoes, 2 Feb. 1937, *Ducke 35657* (G, NY, P); Rio Jandiatuba, from mouth to 10 km upstream, 26 Feb. 1977, *Mori et al. 9131* (NY, U, US). **Mato Grosso Norte:** near scientific center Aripuana, 5 Sep. 1976, *Andrade 3292* (UEC); 200 km NW of Cuiaba, 200 m, 26 Sep. 1963, *Maguire et al. 56867* (F, NY, TEX, US). **Pará:** Belém, 12 Jan. 1928, *Ducke 22543* (NY). **Rio de Janeiro:** São Paulo de Olivença, Rio Solimoes, 2 Feb. 1937, *Ducke s.n.* (U). **Rondônia:** Guajara Mirim, Rio Pacaas Novos, 15 Aug. 1976, *Cavalcante 3297* (MG); between Porto Velho and Cuiaba vicinity of Jarú, 16 Aug. 1968, *Forero & Wrigley 7106* (F, INPA, M, MG, L, U). BOLIVIA. **Beni:** Vaca Diez, Riberalta, 28 Sep. 1923, *Kuhlmann 22541* (NY); junction of Río Beni and Madre de Dios, Aug. 1886, *Rusby 932* (BM, CAS, F, G(2), GH, MO); 20.8 km E of Riberalta on road to Guayaramarín, path on right side, 230 m, 25 Sep. 1981, *Solomon 6433* (MO). **La Paz:** Mapiri, July–Aug. 1892, *Bang 1480* (BM, F, G(2), GH(3)); Mapiri, 570 m, Nov. 1907, *Buchtien 1967* (US); Rurrenabaque, 300 m, 6 Oct. 1921, *White 860* (NY). **Pando:** Madre de Dios, along Río Madre de Dios, 19 km by air from Riberalata, 125 m, 18 Aug. 1985, *Nee 31377* (F, MO, NY); Jatata, forest around the camp of the Western Geophysical, 130 m, 26 July 1992, *Rueda 941* (MO). **Santa Cruz:** Sarah Guaytu forest, 27 Sep. 1917, *Steinbach 347* (G, NY(2)); Río Surutic, 400 m, 2 Oct. 1924, *Steinbach 6544* (BM, F, GH).

Local names and uses. In Bolivia, natives decorate their houses with flowers of this species. It is also used as an ornamental in parks and along avenues. It is called "viuvinha" in Brazil and is used as an ornamental. In Ecuador it is called "pilchi huasca" in Quichua and "kalatara" and "bejuco de calabaza" in Spanish; there the stems and leaves combined with *Usnea* and *Tabernaemontana* are used for birth control and sterilization (Wilbert & Neill, 1987). It is called "yahua-piri-piri" in Peru and is used for snakebites.

This species is related to *P. volubilis* with which it shares a lianaceous habit with axillary aborted racemes and clavate glandular hairs. *Petrea maynensis* is easily separated by its verticillate leaves; *P. volubilis* is opposite-decussate. In addition, the longest petioles of *P. maynensis* do not reach more than 10 mm as in *P. volubilis*.

8. Petrea pubescens Turcz., Bull. Soc. Imp. Nat. Mosc. 36: 211–212. 1863. TYPE: Venezuela. Mérida: near San Cristóbal, 600 m elev., Nov. 1846, *Funck & Schlim 1504* (lectotype, selected by Rueda (1993), BM: isolectotypes, BR, G(2), P, U, W; photo of isolectotype, F, MO, NY, TEX). Figure 20.

Petrea glandulosa Pittier, Bol. Cient. Tecn. Mus. Com. Venez. 1: 70. 1925. TYPE: Venezuela. Portuguesa: near Guanare, Mar. 1924, *Peraza 11532* (lecto-

FIGURE 20. Habit of *Petrea pubescens* Turcz. (*Neill 10014*).

type, selected by Rueda (1993), VEN; isolectotypes, NY, US; photos of lectotype, NY, TEX; photos of isolectotypes, NY, TEX).

Petrea andrei Moldenke, Feddes Repert. 43: 188. 1938. TYPE: Ecuador. 7 Jan. 1877, *André 4707* (holotype, K; fragment of holotype, NY; photos of holotype, NY, TEX).

Petrea pubescens var. *klugii* Moldenke, Feddes Repert. 43: 172. 1938. TYPE: Peru. San Martín: Río Hualaya, Chazuta, elev. 260 m, May 1935, *Klug 4155* (holotype, NY; isotypes, BM, F, GH, MO, S, UC, US).

Petrea scaberrima Moldenke, Feddes Repert. 43: 177. 1938. TYPE: Colombia. Cundinamarca: near Bogotá, 1844–1845, *Purdie s.n.* (holotype, GH; isotype, K; fragment of holotype, NY; photos of holotype, NY, TEX).

Petrea pubescens var. *albicalyx* Moldenke, Phytologia 18: 72. 1969. TYPE: Venezuela. Táchira: N of San Juan de Colón, on hwy. from La Fría to San Cristóbal, from a cultivated plant, 27 Sep. 1967, *Bunting 2369* (holotype, TEX; isotype, TEX).

Tree up to 20 m tall, bole not straight, often oval in cross section; the branchlets slender, brown or grayish, obtusely tetragonal, densely short pubescent. Leaves decussate-opposite or whorled in 3s or 4s; petioles 1–13 mm long, short-pubescent with fulvous or yellowish hairs like the adjacent twigs; blades elliptic, or ovate-elliptic, 3–18.5 cm long, 1.5–9 cm wide, the apex rounded or obtuse, the base attenuate to subacuminate, membranous, rough to touch, often short pubescent on both surfaces. Inflorescences mainly axillary, racemes mostly clustered near the tips of the branchlet, 5–25 cm long, 2–4 cm wide, with aborted racemes in its axils; pedicels 1–10 mm long, densely pubescent, often bearing bractlets to 12 mm long. Flowers with the calyx-tube white or blue, 3–5 mm long, 2–3 mm wide at base, the apex 3.5–5.5 mm wide, densely pubescent, 5-lobed, the lobes membranous, obovate or elliptic, 11–18 mm long, 2–5 mm at the widest point, acute or blunt at apex, glabrous; calycinal crest with the lobes ca. 1.5 mm long and wide, the apex sharply acute, translucent and ciliate on the margins, pubescent; corolla-tube 6–7 mm long, the base 1.5–3 mm wide, ampliate to 4–5.5 mm at apex, pubescent, the limb sometimes with white-blue dots, rotate, 5-lobed, the anterior lobe largest, the remaining lobes similar, but smaller; stamens 4; filaments 1.5–2 mm long, glabrous; anthers 1 2 mm long, 0.4–1.2 mm wide; staminode sometimes present; ovary globose, 1–1.5 mm long, 1 -2 mm wide, glabrous; style ca. 18–25 mm long, pubescent; stigma subcapitate.

Distribution (Fig. 8). This species is found from northern South America south to northern Bolivia, and northwestern Brazil. This species has been collected at 2200 m elevation, representing the highest altitude for any recorded collection of the genus.

Selected specimens examined. COLOMBIA. **Antioquia:** Medellín, 22 Apr. 1927, *Toro 242* (NY, US). **Cauca:** Río Quilichao, between Santander and San Pedro, 1150 m, 5 Oct. 1954, *Fernandez 2768* (COL); La Paila, 23 Aug. 1853, *Holton 572* (GH). **Cundinamarca:** Fusagasugá, Boquerón de Fusa, 400 m, 20 Aug. 1975, *López-Palacios & Idrobo 3693* (COL, NY, TEX, S); Girardot, between Girardot and Melgar, near El Paso, 420 m, 7 Aug. 1939, *Perez & Cuatrecasas 6577* (COL, NY, US). **Huila:** Neiva, 18 June 1961, *Schwabe s.n.* (B); San Alfonso, Aug. 1934, *Guevara 2E* (US). **Magdalena:** Manaure, Sierra de Santa Marta, 960 m, 25 Aug. 1946, *Foster & Foster 1591* (COL), 1898–1901, *Smith 1521* (BR, BM, F, G(2), GH(3), LE, U, UC). **Meta:** Jan. 1937, *García 5206* (COL, US); La Macarena, at the junction of the rivers Sansa and Guejar, margin of Río Guejar, 490 m, 22 Feb. 1956, *Idrobo 2041* (COL). **Norte de Santander:** Pamplona, 1842–1843, *Linden 1357* (BM(2), G(3), GH, W(2)). **Putumayo:** Umbría, 325 m, Dec. 1930, *Klug 1894* (BM, F, GH(2), MO). **Santander:** between Cucuta and Pamplona, along Río Pamplonita, near La Donduana, 700 m, 25 July 1940, *Cuatrecasas & García 10173* (COL, US). **Tolima:** San Luis, near Corregimiento de Payande, 1300 m, 13 Mar. 1965, *García-Barriga 18167* (COL, GH, US); Lerida, 1300 m, 14 Mar. 1965, *García-Barriga 18182* (COL, GH, NY, US). **Valle de Cauca:** Dagua, drainage of upper Dagua Valley, 14 km above Dagua, on road to Cali, 1500 m, 25 Nov. 1963, *Hutchison & Wright 3271* (BR, F, G(2), GH, LE, M, MO, UC). VENEZUELA. **Amazonas:** Puerto Ayacucho, Atures, on road to El Burro, 6 km N or Puerto Ayacucho, 5 Apr. 1984, *Plowman 13497* (F, MO, NY, U). **Apure:** Rómulo Gallegos, Caño Caribe, ca. 19 airline km SW of Elorza, 90 m, 8 Mar. 1979, *Davidse & González 6214* (MO, SP, TEX). **Aragua:** 12 km S of San Casimiro, 6 June 1967, *Robertson 152* (MO). **Barinas:** Pedraza, Feb. 1953, *Aristeguieta 1602* (NY), Apr. 1959, *Aristeguieta 3864* (NY); 850 m, 4 June 1957, *Bernardi 6350* (G(2)). **Bolivar:** Cedeño, near Caño Villaca, road Caicara to El Burro, 18 Apr. 1984, *Stergios et al. 8570* (MO(2), PORT). **Carabobo:** Hwy. Valencia to Puerto Cabello, 21 Apr. 1976, *Guevara 2288* (BM). **Lara:** Moran, 20 km N of Guárico on road to Villanueva, 1200 m, 5 Mar. 1983, *Aymard et al. 1864; 1865* (PORT), 3–4 km NE of Sicarigua, along Panamerican hwy., 140 m, *Gentry et al. 11010* (MO, US). **Mérida:** 26 June 1956, *Bernardi 3331* (NY); Tovar, road San Francisco–Guaraque, 1600 m, 10 May 1967, *Berti 1722* (BR, U). **Portuguesa:** Guanare, 26 Feb. 1981, *Aymard 99* (NY, PORT); Ospinos, 10 km N of La Estación, 700 m, 25 June 1984, *Aymard 2585* (PORT). **Táchira:** around San Cristóbal, Mar. 1960, *Aristeguieta-Agostini 4113* (AAU, U(2)); road La Fría–San Cristóbal, N of San Juan de Colón road, 27 Sep. 1967, *Bunting 2369* (TEX). **Trujillo:** Carache del Río, between Las Peñas and Las Palmas, 1 Dec. 1979, *Benitez 2659* (F); between Timotes and La Puerta, 1700 m, 20 Mar. 1969, *Oberwinkler 15144* (M). ECUADOR. **Morona–Santiago:** Morona, Cordillera de Cutucu, road Méndez Morona, 800 m, 4 Feb. 1989, *van der Werff & Palacios 10417* (MO). **Napo:** Orellana, 20 km S of Coca, on Via Auca, toward Río Tiputini, 270 m, 20 Nov.

1991, *Neill & Rojas 10014* (MO); 15 km S of Coca, 225 m, 4 Aug. 1992, *Rueda et al. 1010* (MO). **Zamora-Chinchipe:** Zamora, E slope of the Cordillera, valley of the rivers Negro and Chupianza, 550 m, 12 Dec. 1944, *Camp E-1450* (NY, US). PERU. **Huanuco:** Puerto Inca, Yayapichis, Unidad Modelo de Manejo y Producción Forestal Dantas, 270 m, 1–15 Dec. 1989, *Flores & Tello 47* (MO). **Madre de Dios:** Tahuamanu, Iberia, Río Tahuamanu, 330 m, 4 Sep. 1945, *Seibert 2164* (MO, US). **San Martín:** Huallaga, Chazuta, Río Huallaga, 260 m, May 1935, *Klug 4155* (F, GH, MO, NY, S, UC). BRAZIL. **Acre:** Río Acre, Aug. 1911, *Ule 9722* (G(2), NY(2), US). BOLIVIA. **Pando:** 54 km SW of Cobija, 250 m, 24 July 1988, *Pennington et al. 35* (LPB).

Local names and uses. It is named "pluma" and "chaparro" in Colombia and "penitente" in Venezuela. It is widely cultivated as an ornamental in Venezuela.

This species is similar to *P. rugosa*, but the latter is primarily a shrub that does not reach more than 5 m, as opposed to *P. pubescens*, a tree reaching up to 20–25 m. The leaves of *P. pubescens* tend to be whorled rather than opposite-decussate as in *P. rugosa*. The mature leaves in the latter species are bullate as opposed to smooth in *P. pubescens*. Flowers with white calyces are known for this species from both wild and cultivated plants.

9. Petrea rugosa Kunth, Nov. Gen. Sp., 2: 282. 1818. TYPE: Venezuela. Distrito Federal: Caracas, *Humboldt & Bonpland s.n.* (lectotype, selected by Rueda (1993), P-HB; isolectotypes, F, P; photos of lectotype, TEX, US; photos of isolectotypes, F, MO, NY(2), TEX). Figure 21.

Petrea obtusifolia Benth., Pl. Hartw. 1846. TYPE: Colombia. Tolima: 1843, *Hartweg 1359* (lectotype, selected by Rueda (1993), K; isolectotypes, BM, G, K; fragment of isolectotype, NY; photos of lectotype, NY, TEX).

Petrea rugosa var. *casta* Moldenke, Feddes Repert. 43: 48. 1938. TYPE: Panama. Canal Zone: from a cultivated plant, 2 Dec. 1936, *Lindsay 452* (holotype, NY).

Shrub to 3 m tall; the branchlets obtusely tetragonal, pubescent. Leaves with petioles 1–6 mm long, pubescent; blades elliptic to oblong, 3–11 cm long, 2.5–8 cm wide, the apex obtuse, or rounded, the base rounded or obtuse, membranous, rough to the touch on both surfaces, pubescent especially beneath, mature leaves bullate. Inflorescences mainly axillary, abundant, racemes 12–45 cm long, 3–6 cm wide; pedicels 1–10 mm, pubescent. Flowers with the calyx blue or white, calyx-tube ca. 6 mm long, ca. 2 mm wide at base, ca. 4 mm wide at apex, short-pubescent, 5-lobed, obovate, 10–13 mm long, ca. 3 mm wide at base, 5–7 mm wide at the widest point; calycinal crest with the lobes ca. 1.5 mm long, and 2 mm wide at base, acute at apex, puberulent; corolla blue or white, the tube 8–11 mm long, the base ca. 2 mm wide, ampliate, to 4–6 mm at apex, the anterior lobe largest, broadly elliptic, ca. 6 mm long, ca. 7 mm wide, the remaining lobes ca. 5 mm long, ca. 6 mm wide, puberulent; stamens 4; filaments ca. 1.5 mm long, pilose; anthers ca. 1.5 mm long, ca. 0.5 mm wide; ovary ca. 1.2 mm long and wide, glabrous; style ca. 3 mm long, glabrous; stigma subcapitate.

Distribution (Fig. 11). This species occurs in Colombia and Venezuela, growing in mountain savanna with shrubby growth, or on open rocky slopes, at altitudes of up to 1700 m.

Selected specimens examined. COLOMBIA. **Antioquia:** San Jerónimo, 900 m, July 1968, *Barkley 38C494* (TEX); Segovia, 750 m, 18 June 1979, *Rentería et al. 1630* (COL). **Caldas:** La Dorada, 250 m, 18 Dec. 1936, *Haught 2103* (F, GH, NY, S, US(2)); Victoria, Río Guarino, 200 m, 5 June 1970, *Uribe 6442* (COL, NY, US). **Cauca:** Rosas, La Esperanza, 11 Sep. 1975, *López-Palacios & Idrobo 3831* (COL, NY, TEX). **Cundinamarca:** Silvania, S of Silvania on toll road to Fusagasugá, near km 37 turn W and proceed for 1 km on road to Tibacuy, 1400 m, 26 May 1972, *Barclay et al. 3461* (COL); Fusagasugá, Feb. 1860, *Lindig 620* (P). **Huila:** Garzón, Vereda de Las Quebraditas, 900 m, 21–26 Feb. 1947, *Bermudez 34935* (UC); Garzón–Zuloaga road, 1400 m, 29 Sep. 1976, *Echeverry 194* (COL). **Magdalena:** 600 m, Dec., *Lehmann 8645* (GH(3), L, NY(2), US); 400 m, 1851–1857, *Triana s.n.* (US). **Meta:** 6 km SE of Altamira along road to Florencia, mountain savanna with shrubby growth in gullies, 800 m, 9 Jan. 1974, *Davidse et al. 5599* (COL, MO, TEX). *Tolima:* Honda, Aug. 1919, *Ariste-Joseph, Bro s.n.* (US); Mariquita, 6 Jan. 1948, *Schneidern 512* (S); Purificación, valley of the Magdalena river, 1843, *Hartweg 1359* (BM, G, K(2), NY). **Valle de Cauca:** Cali, 1000 m, 15 June 1938, *Duque-Jaramillo 4340-A* (COL); Palmira, 2 May 1935, *Archer 3358* (US). **Valparaiso:** Murillo, 1000 m, 7 Mar. 1938, *Dryander 2303* (BM, US). VENEZUELA. **Táchira:** Capacho, between El Monumento Cristo Rey and La Zona Militar, 1650 m, 12 Aug. 1985, *Bond 5080* (MO). **Distrito Federal:** Caracas, *Humboldt & Bonpland s.n.* (P(2)).

Local names and uses. ***Petrea rugosa*** is known as "azulino carrasposo," "azulito," "chaparrito," "chaparrillo," "heliotropo blanco," "mamoncillo," "pavita," "pluma del rey," "pluma de la reina," "plumilla," and "sombrerito" in Colombia, where it is used as an ornamental.

It is closely related to *P. pubescens* (see discussion under that species). Occasional plants of this species with white flowers, or at least with white calyces, are known both wild and in cultivation.

FIGURE 21. *Petrea rugosa* Kunth (*García 6472*).—A. Habit.—B. Close-up of abaxially bullate leaf surface.

10. Petrea sulphurea M. J. Jansen-Jacobs, Flora Guianas 4: 60–63. 1988. TYPE: French Guiana. Piste de St. Laurent à Paul Isnard, 15 Nov. 1982, *Granville 5341* (holotype, CAY; isotypes, BR, P, U). Figure 22.

Liana; the branchlets tetragonal, winged, often twisted, pubescent, some of the hairs glandular. Leaves with petioles 5–11 mm long; blades elliptic, 3.5–15 cm long, 2.5–7 cm wide, the apex acute and apiculate, the base acute or broadly acute, coriaceous, asperous, glabrous above except on the primary vein, minutely pubescent and glandular dotted beneath. Inflorescences terminal, racemes 9–16 cm long; bracts narrowly ovate, 5–10 mm long; bractlets one pair on the pedicels, setaceous, 1–2 mm long; pedicels 1–3 mm long. Flowers with the calyx-tube 6–8 mm long, the lobes rounded or apiculate, unequal, 2 lobes narrowly elliptic-oblong, ca. 20 mm, ca. 6 mm wide, acute-obtuse, 3 lobes broadly ovate, ca. 5 mm long, ca. 6 mm wide, acute-acuminate, greenish, short-pubescent; calycinal crest 5-cleft, the lobes ca. 2 mm long, pubescent; corolla yellow, 2–3 cm long, the lobes

FIGURE 22. Habit of *Petrea sulphurea* M. J. Jansen-Jacobs (*Granville 5341*).

rounded, ca. 0.5 cm long, glandular pubescent; stamens 4; filaments 7–10 mm long, glandular pubescent around the insertion; anthers ca. 2 mm long, glabrous; ovary oblong, ca. 1 mm long, glabrous; style 17–20 mm long, glabrous, stigma subcapitate.

Distribution (Fig. 10). *Petrea sulphurea* is only known from a very narrow area in French Guiana, growing in clearings in primary forest.

Specimens examined. FRENCH GUIANA. km 80 Piste de St. Laurent à Paul Isnard, 15 Nov. 1982, *Gran-*

ville 5341 (BR, CAY(2), P, U); km 40 Piste de St. Laurent à Paul Isnard, between Citron and Le Guet de la Crique Mousse, 15 Nov. 1982, *Billiet & Jadin 1705* (BR).

Local names and uses. None reported.

This is a distinctive species in the cladistic analysis but close to the clade where *P. bracteata* is found. *Petrea sulphurea* is similar to the latter species in having the longest pedicels in the genus, more than 15 mm long, and petioles with two lateral traces. However, *P. sulphurea* has calyx lobes of two sizes whereas they are equal in *P. bracteata*. It also shares with *P. insignis* a pair of bractlets on the floral pedicels. While both *P. insignis* and *P. bracteata* have blue flowers, *P. sulphurea* is the only species in the genus with yellow flowers.

11. Petrea volubilis L., Sp. Pl., ed. 1: 626. 1753. TYPE: Netherlands. Hartecamp, cultivated in George Clifford's garden from material from Veracruz, Mexico, 1735–1737, *Linnaeus s.n.* (holotype, BM, herb. Linnaeus 781.1; photos of holotype, MO, TEX). Figure 23.

Petrea arborea Kunth, Nov. Gen. Sp., 2: 282–283. 1818. TYPE: Venezuela. Aragua: near Cura, near Guacara and Hacienda de Cura, 1800, *Humboldt & Bonpland s.n.* (lectotype, selected by Rueda (1993), P).

Petrea racemosa Nees, Flora 4: 300. 1821. TYPE: Brazil. Bahía: Rio Grande de Belmonte, 23 July–21 Dec. 1816, *Wied-Neuwied s.n.* (lectotype, selected by Rueda (1993), BR; isolectotype, G; photos of lectotype, MO, NY, TEX).

Petrea mexicana Cham., Linnaea 7: 367. 1832. TYPE: Mexico. Tamaulipas: Tampicos, 1829, *Berlandier 136* (lectotype, selected by Rueda (1993), G; isolectotype, L; photo of lectotype, TEX).

Petrea subserrata Cham., Linnaea 7: 368. 1832. TYPE: Brazil. *Sellow s.n.* (lectotype, selected by Rueda (1993), K; photo-isolectotype, US).

Petrea kohautiana C. Presl, Bot. Bemerk. 99. 1844. TYPE: Windward Islands. Martinique, 1819–1821, *Kohaut s.n.* (lectotype, selected Rueda (1993), BR; isolectotypes, B(2), F, G, L, M; fragment of isolectotype, NY; photo of isolectotype, GH).

Petrea ovata M. Martens & Galeotti, Bull. Acad. Roy. Sci. Belgique 11: 329. 1844. TYPE: Mexico. Veracruz: Jalapa, Aug. 1940, *Galeotti 793* (lectotype, selected by Rueda (1993), BR; isolectotypes, BR, G(2), GH, LE, U, US; fragment of isolectotypes, NY; photo of lectotype and isolectotype, TEX).

Petrea aspera Turcz., Bull. Soc. Imp. Nat. Mosc. 36: 211. 1863. TYPE: Venezuela. Carabobo: San Estevan, 300 m elev., Apr. 1845, *Funck & Schlim 507* (lectotype, selected by Rueda (1993), BR; isolectotypes, BM, G(2), P, W; fragment of isolectotype, US; photos of isolectotype, F, MO, NY(2), TEX, U, W).

Petrea vincentina Turcz., Bull. Soc. Imp. Nat. Mosc. 36: 212. 1863. TYPE: Windward Islands. St. Vincent, *Caley s.n.* (lectotype, selected by Rueda (1993), G; isolectotype, G; photo of isolectotype, NY).

Petrea fragrantissima Rusby, Mem. New York Bot. Gard. 7: 338. 1927. TYPE: Bolivia. La Paz: Rurrenabaque, 300 m elev., Oct. 1921, *Rusby 860a* (holotype, NY; isotype, TEX).

Petrea volubilis var. *albiflora* (Standl.) Moldenke, Revista Sudamer. Bot. 5: 2. 1937. TYPE: Belize. Sitte river, 17 Mar. 1931, *Schipp 727* (holotype, F; isotypes, BM, G, MICH, MO, NY, S; photo of holotype, TEX).

Petrea amazonica Moldenke, Feddes Repert. 43: 173. 1938. TYPE: Brazil. Amazonas: mouth of the Rio Embira, 19 June 1933, *Krukoff 4930* (holotype, NY; isotypes, G, GH, K; photos of isotype, NY, TEX).

Petrea arborea var. *broadwayi* Moldenke, Feddes Repert. 43: 26. 1938. TYPE: Trinidad. St. Ann's, 1908, *Broadway s.n.* (holotype, UC; isotype, MO; photos of holotype, NY, TEX).

Petrea atrocoerulea Moldenke, Feddes Repert. 43: 195. 1938. TYPE: Colombia. Antioquia: Río Porce, 7 May 1980, *Kalbreyer 1634* (lectotype, selected by Rueda (1993), K; fragment-isolectotype, NY; photo-isolectotypes, NY, TEX).

Petrea colombiana Moldenke, Feddes Repert. 43: 174. 1938. TYPE: Colombia. Santander Sur: Bucaramanga, from a cultivated plant, 1000 m elev., 8 Feb. 1927, *Killip & Smith 19067* (holotype, GH; isotypes, GH, NY, US; photos of holotype, NY, TEX).

Petrea kohautiana var. *anomala* Moldenke, Feddes Repert. 43: 31. 1938. TYPE: Trinidad. St. Clair, May 1911, *Broadway s.n.* (holotype, NY).

Petrea nitidula Moldenke, Feddes Repert. 43: 168. 1938. TYPE: Brazil. Amazonas: near Panuré, Rio Uaupés, Oct. 1852–Jan. 1853, *Spruce 2926* (holotype, G; isotypes, BM, BR, F, G, GH, LE, NY; photos of holotype, NY, TEX; photos of isotype, F, MO).

Petrea riparia Moldenke, Feddes Repert. 43: 194. 1938. TYPE: Brazil. Pará: São Luis, Rio Tapajos, 6 Dec. 1915, *Ducke 15822* (holotype, G; isotype, BM; fragment of isotype, NY; photos of holotype, NY, TEX).

Petrea rivularis Moldenke, Feddes Repert. 43: 191. 1938. TYPE: Guyana. Waini river, Nov. 1910, *Anderson s.n.* (holotype, K; isotype, K; fragment of holotype, NY; photo of holotype, TEX).

Petrea swalleni Moldenke, Feddes Repert. 43: 192. 1938. TYPE: Brazil. Pará: Boa Vista, Rio Tapajos, 7–13 Jan. 1934, *Swallen 3127* (holotype, US; isotype, NY; photos of holotype, NY, TEX).

Petrea volubilis var. *pubescens* Moldenke, Feddes Repert. 43: 45. 1938. TYPE: Honduras. Comayagua: San Luis, 6 May 1933, *Edwards P601* (holotype, US; isotypes, BR, F; photo of holotype, TEX).

Petrea aspera f. *albiflora* Moldenke, Phytologia 18: 421. 1969. TYPE: Panama. San Blas: 23 Apr. 1933, *Cooper 234* (holotype, NY).

Liana, sometimes shrubby with stem ca. 10 cm DBH; the branchlets obtusely tetragonal, pubescent or glabrous. Leaves decussate-opposite, rarely some whorled; petioles 1–16 mm long, sometimes pubescent; blades elliptic, 3–25 cm long, 1.4–11 cm wide, the apex short-acuminate, the base rounded or acute, entire, sometimes serrate or denticu-

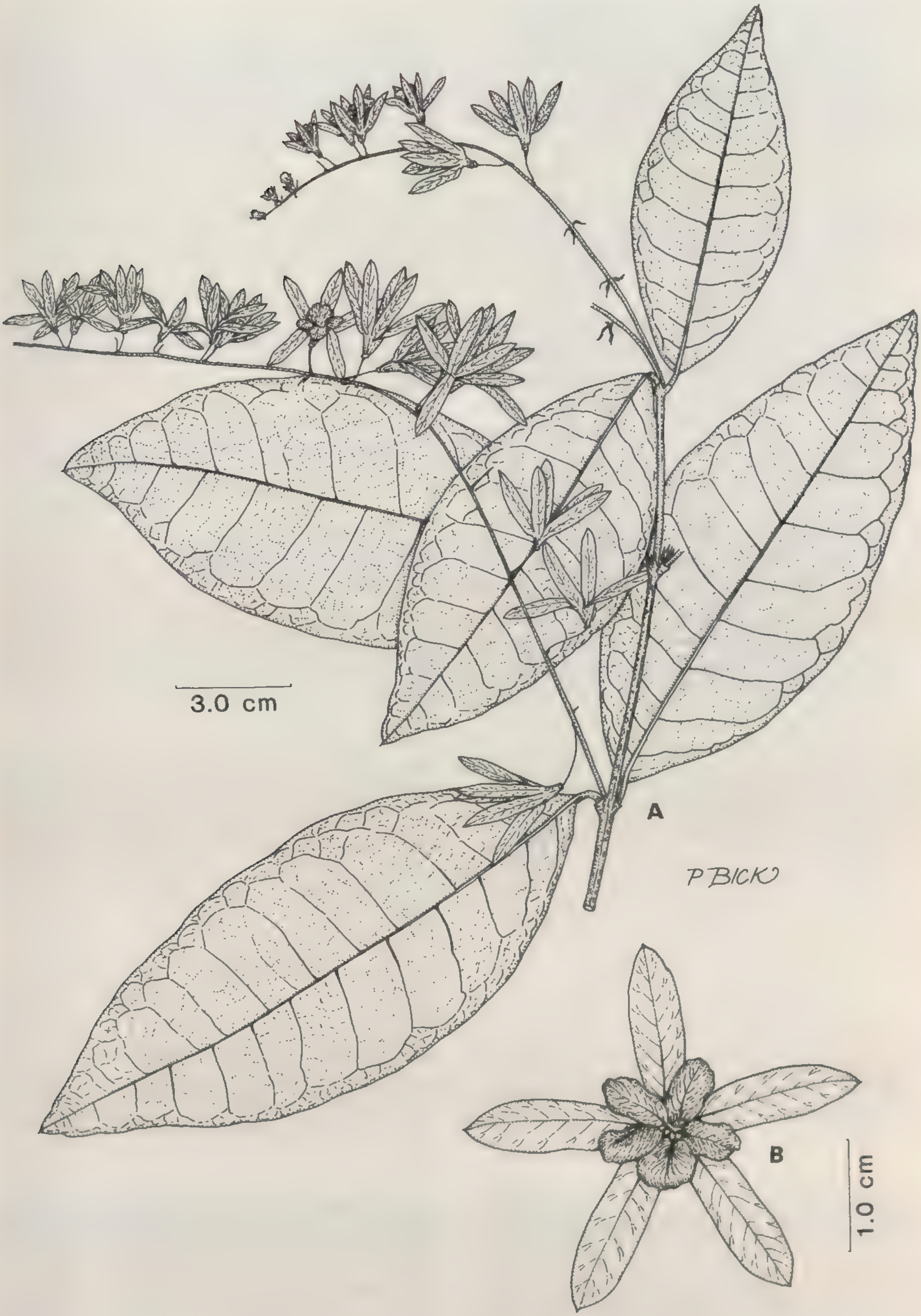


FIGURE 23. *Petrea volubilis* L. (*Martínez 11375*).—A. Habit.—B. Flower.

late, asperulous, rough to the touch, glabrous or pubescent. Inflorescences axillary, racemiform, 4–58 (> 80 cm in cultivated plants) cm long, 1.5–9.5 cm wide, with aborted racemes in the axils; pedicels 10–35 mm long; a bractlet lanceolate, sometimes borne on the pedicel, 4–7 mm long, 1–2 mm wide. Flowers with the calyx white or blue, calyx-tube 3–7 mm long, 2.5–5 mm wide at base, 2.5–7 mm wide at apex, glabrous or pubescent, 5-lobed, the lobes membranous, oblong, 8–29 mm long, 2–10 mm wide, the apex rounded; calycinal crest with the lobes 1.2–2.5 mm long and 1.5–2 mm wide, ciliate on the margins, the apex acute; corolla blue or white, fragrant, 6–15 mm long, the base 1.5–3 mm wide, conspicuously ampliate to 3–9 mm at apex, pubescent, the limb rotate, 5-parted, the anterior lobe largest, sometimes punctate and with white spots, puberulent, the remaining lobes similar, but smaller; stamens 4, didynamous to homodidynamous; filaments 1.2–2 mm long, glabrous; anthers ca. 1.5 mm long, ca. 0.8 mm wide, pilose; staminode ca. 1 mm long sometimes present; ovary oblong, 1.2–3.5 mm long, 1.5–2.5 mm wide, glabrous; style 2–4 mm long, glabrous; stigma subcapitate.

Distribution (Fig. 5). This is the most widely distributed species in the genus. It ranges from the southern half of Mexico throughout the West Indies to Peru and Paraguay. It grows in seasonal evergreen forest along streams, roadsides, steep limestone walls in dry forest, limestone outcrops, pastures on clay and rocky soil, and on rock. In Mexico it has been reported growing with such genera as *Brosimum, Capparis, Ceiba, Tabebuia,* and *Trichilia* (i.e., sub *Breedlove 49633*), and the flowers are visited by honeybees (sub *Nee & Taylor 26607*).

Selected specimens examined. MEXICO. **Campeche:** Champotón, 20 km N of Ruinas Edzna, 29 Mar. 1982, *Cabrera & Cabrera 2348* (BM, MEXU). **Oaxaca:** Tuxtepec, Cerro Buenos Aires, W of La Presa Temazcal, 60 m, 6 Mar. 1986, *Cortéz et al. 197* (MEXU). **Quintana Roo:** km 4 Chetumal-Bacalar road, 4 Mar. 1958, *Schubert & Gómez 1686* (GH, MEXU). **Tabasco:** Balancán, on road to El Triunfo, 3 Nov. 1976, *Méndez 441* (MO). **Veracruz:** Actopan, on road to Cerro de la Mesa, 1 km from Mozomboa, 50 m, 16 Apr. 1985, *Acosta & Acosta 245* (CHAPA). **Yucatan:** Tizimín, Dzonot Ake Community, 24 km of Tizimín, 25 Feb. 1986, *Aguilar et al. 130* (MEXU). GUATEMALA. **Alta Verapaz:** Río Cahabon, Finca Canihor, 250 m, 5 Apr. 1940, *Stuart 36* (MICH). **Izabal:** Lake Izabal, 22 May 1966, *Snedaker D67* (F, GH). **Petén:** Tikal National Park, S of the Hotel Posada La Selva, 18 Mar. 1970, *Tun 785* (F, S, WIS). **Santa Rosa:** Aguas Calientes, 23 Jan. 1908, *Kellerman 7738* (F). **Zacapa:** Loma El Picacho, above Santa Rosalia, 1400 m, 15 Jan. 1942, *Steyermark 42728* (F). BELIZE. **Belize:** Gracie Rock, 1.5–4 mi. S of mi. 22 on western hwy., 100 m, 21 Jan. 1974, *Liesner & Duyer 1498* (MO, US). **Orange Walk:** on path between Lago Tan and N of San Antonio Village, July 1973, *Leino 223* (MO). **Toledo:** trail to Esperanza, beginning 1 mi. N of Columbia forest station, 12 June 1973, *Dwyer 11132* (MO). HONDURAS. **Atlántida:** La Ceiba, 10 May 1985, *Bados 174* (MO). **Colón:** road to Castilla, 2.5 mi. E of Trujillo, 22 Apr. 1980, *Saunders 196* (BM, F, MO, NY). **El Paraíso:** near Danlí, 14 Apr. 1970, *Barkley & Barkley 40156* (MO, TEX). **Yoro:** 5 km E of Morazán, on road to Yoro, 21 May 1987, *Blackmore & Chorley 4035* (BM). EL SALVADOR. **San Vincente:** 400 m, 2–11 Mar. 1922, *Standley 21187* (GH, MO, NY, US). **Santa Ana:** Hacienda San Miguel, near Metapan, Summit of Cerro El Pinal, 1000 m, 22 Feb. 1946, *Carlson 849* (F). NICARAGUA. **Carazo:** Quebrada La Chota, ca. 7 km NE from Chacocente biological station, 100 m, 19 Mar. 1983, *Grijalva 2430* (HNMN). **Jinotega:** vicinity of Jinotega, 1070 m, 19 June–9 July 1947, *Standley 10065* (F). **Zelaya:** Siuna, vicinity of La Luz, 175 m, 14 Mar. 1961, *Bunting & Licht 649* (NY, F, US). COSTA RICA. **Alajuela:** San Ramón, Los Angeles, 28 Mar. 1931, *Brenes 13620* (NY). **Guanacaste:** along Panamerican hwy., near Nicaraguan frontier, 100 m, 11 Mar. 1976, *Fallon & Solomon 2636* (MO). **Heredia:** Sarapiquí, La Selva biological station, the OTS field station on the Río Puerto Viejo, just E of its junction with Río Sarapiquí, 100 m, 12 Jan. 1982, *Oberbauer 101* (F, U). **Puntarenas:** Monteverde, Valle del Río de San Luis, 900 m, 28 Apr. 1989, *Bello 827* (MO). PANAMA. **Colón:** Canal Area, Barro Colorado Island, shoreline of Colorado peninsula, 13 May 1968, *Croat 5538* (MO). **Darién:** Punta Guayobo Grande, along beach and approximately 50 m from water edge, 25 m, 20 Apr. 1980, *Antonio & Hahn 4247* (MO, TEX). **Panamá:** Serranía de Maje, between Charco Rico and trail along Río Ipeti Grande, confluence with Río Agua Fría, 300 m, 28 Jan. 1984, *Churchill & Nevers 4436* (MO). **San Blas:** El Llano–Cartí road, 2 Mar. 1986, *Nevers 7231* (MO). **Veraguas:** San Francisco, Feb. 1924, *Powell s.n.* (US). CUBA. **Cienfuegos:** 10 Mar. 1926, *Jack 4249* (US). **Santiago:** 18 Apr. 1902, *Hamilton 127* (NY). JAMAICA. Ca. 2 mi. NW of Mandeville, 600 m, 5 Mar. 1980, *Proctor 38629* (NY). DOMINICAN REPUBLIC. Guazumal, 10 Feb. 1946, *Jímenez 1028* (US). PUERTO RICO. Naguabo, 12 Mar. 1965, *Wagner 786* (GH). LEEWARD ISLANDS. **Antigua:** Dunning Valley, 5 Sep. 1937, *Box 1033* (BM, F). **Guadeloupe:** 1944–1946, *Bena 1227* (P). COLOMBIA. **Amazonas:** Leticia, forest near outskirts of town on Brazilian frontier, 17 Nov. 1974, *Gentry 12728* (MO, TEX). **Antioquia:** Turbo, Corregimiento de Lomas Aisladas, 50 m, 8 Feb. 1985, *Rentería et al. 3615* (MO). **Bolívar:** San Juan de Nepomuceno, Loma Los Colorados, 200 m, 2 Sep. 1986, *Cuadros 3130* (MO). **Chocó:** Los Kativos National Park, NE of Tilupo, 160 m, 6 Mar. 1976, *Forero & León 120* (MO). **Santander:** Barranca Bermeja, Magdalena valley, between Sogamoso and Colorado rivers, 300 m, 19 Feb. 1935, *Haught 1568* (US). VENEZUELA. **Amazonas:** Atabapo, Quebrada El Grillo, *Steyermark 129383* (COL). **Aragua:** Henri Pittier National Park, N from Maracay, 700 m, 9 Feb. 1969, *Oberwinkler 14704* (M). **Bolívar:** Campamento La Yagua, ca. 24 km NE of Caserio Los Rosos, 16–25 June 1965, *Blanco 145* (MO). **Miranda:** Distrito Páez, between Río Guapo and drainage of the Río Guapo, 300 m, 1–2 June 1977, *Davidse & González*

13511 (MO, U). **Zulia:** Lagunillas, along Río Grande, 13 km N of Embalse, 600 m, 1–5 Apr. 1982, *Bunting et al. 11278* (NY, TEX). TRINIDAD. St. Ann's, Hololo mountains road, 24 Apr. 1930, *Broadway 7568* (BM, F, G(2), E. MO, UCLA). GUYANA. Essequibo, Itanime Falls, Essequibo river, 29 Sep. 1937, *Smith 2148* (GH, NY). SURINAME. Nickerie, area of Kabalebo dam project, at km 16.5, 7 km E of Ferry over Kabalebo, 20 Nov. 1976, *Heyde & Lindeman 229* (U). FRENCH GUIANA. St. Laurent, above mouth of Maroni river, island in Moroni river, near Antecum Pata, 140 m, 21 Aug. 1987, *Weitzman 243* (MO). PERU. **Amazonas:** Bagua, road between Chiviaco and El Muyo, both sides of the road, 500 m, 19 Nov. 1990, *Díaz & Amaro 4261* (F). **Loreto:** Maynas, Mishana, trail from village to Campamento 1, 140 m, 22 July 1980, *Gentry et al. 28928* (MO). BRAZIL. **Amazonas:** Vila Bittencourt, left margin of Rio Japura, 14 Nov. 1982, *Amaral et al. 446* (NY). **Bahía:** Rio Jequitionha, in the road to Itaimbe, 7 Apr. 1971, *Santos 1580* (TEX). **Minas Gerais:** Carmo do Rio Claro, Fazenda Novo Horizonte, 28 Aug. 1961, *Andrade 951* (R). **Pará:** Paimeru, Parque Indigena de Tumucumaque, Rio Paru do Oeste, Missão Tiriyo, 16 Feb. 970, *Cavalcante 2392* (NY, TEX). **Paraná:** Cerro Azul, Rio Turvo, 5 Oct. 1977, *Hatschach 40343* (NY). BOLIVIA. **Beni:** Rurrenabaque, 300 m, Oct. 1921, *Rusby 860A* (NY, TEX). PARAGUAY. May, *Hassler 11234* (G(3), GH). ECUADOR. **Morona–Santiago:** Santiago, Taisha, 500 m, 3 Feb. 1962, *Cazalet & Pennington 7649* (B, NY, UC, US). **Napo:** Yasuni National Park, Pozo Amo 2, trail to Río Daymi, 230 m, 14 Jan. 1988, *Cerón 3320* (MO).

Local names and uses. Because of the wide distribution of *Petrea volubilis*, it is known by numerous common names: Brazil, "cipó de São Miguel," "flor de São Jose," "flor de São Miguel," "flor de viuva," "jasmin roxo," "toucado de viuva," "viuvinha"; Colombia, "chaparro"; Costa Rica, "choreque"; Honduras, "chaparro," "flor del diablo," "flor de Jesus," "lengua de vaca," "lija," "manto del nazareno," "raspa guacal," "sombrerito"; El Salvador, "adolfina," "flor de Jesus," "manto de Jesus"; French Guiana, "kaytapoa," "mayapi"; Mexico, "aax," "bejuco de lija," "bejuco de soltero," "bejuco lava plato," "bejuco pan tostado," "bejuco tieso," "capitan lila," "espuela de caballero," "piocha vieja," "raspa sombrero," "Santa Rita," "thathup ts'aah," "tochpzimin," "tuchicon," "veracuza," "xob-tzimin," "yoch opp tzi min," "yoxop jimin"; Nicaragua, "machigua"; Panama, "bejuco de ajo," "flor de niño"; United States, "purple wreath," "queen wreath"; Venezuela, "bejuco de mayo," "bejuco de palo," "flor de mayo," "moradito," "nasareno," "sandpaper vine," "Santa Lucia," "serae serae," "tostadito," "tukuinamedu"; West Indies, "fleur de la fete de dieu," "flor de papel," "liane rude," "liane de St. Jean." This species is mostly used as an ornamental; it is cultivated worldwide. In Mexico the leaves are used to feed domestic animals such as horses and cows, and in Venezuela the wood is used to make toys.

Petrea volubilis is closely related to *P. maynensis* (see discussion under that species). White flowers are known from this species in some cultivated plants. This species is highly variable in leaf and flower size, habit and indument, the reason for the numerous synonyms throughout its range. The continuity of this variation can be clearly seen when the material from the entire distribution is observed.

Literature Cited

Abu-Asab, M. S. & P. D. Cantino. 1987. Phylogenetic implications of leaf anatomy in subtribe Melittidinae (Labiatae) and related taxa. J. Arnold Arbor. 68: 1–34.

Agardh, J. G. 1858. Theoria Systematis Plantarum. C. W. K. Gleerup, London.

Aiton, W. T. 1812. Hortus Kewensis, 2nd ed., Vol. 4. Longman, Hurst, Rees, Orme and Brown, London.

Andray, C., R. Wylde, C. Lafitte, G. Privat & F. Winternitz. 1982. Structures of verbascoside and orobanchoside, caffeic acid sugar esters from *Orobanche rapumgenistae*. Phytochemistry 21: 1123–1127.

Ayensu, E. S. 1981. Medicinal Plants of the West Indies. Reference Publications, Michigan.

Bentham, G. & J. D. Hooker. 1876. Genera Plantarum. Reeve, London.

Briquet, J. 1895. Verbenaceae. Pp. 132–182 *in* A. Engler & K. Prantl (editors), Die Natürlichen Pflanzenfamilien, Teil 4, Abt. 3a. W. Engelman, Leipzig.

Cantino, P. D. 1990. The phylogenetic significance of stomata and trichomes in the Labiatae and Verbenaceae. J. Arnold Arbor. 71: 323–370.

Carlquist, S. 1988. Comparative Wood Anatomy. Springer-Verlag, Berlin.

Echeverry, R. 1984. Flora Apicola Colombiana. Litografia Arco, Bogotá.

Farris, J. S. 1988. Henning86. Version 1.5. Documentation published by the author. State University of New York, Stony Brook.

———. 1989. The retention index and the rescaled consistency index. Cladistics 5: 417–419.

Garnier, J., J. Mahuteau, M. Plat & C. Sastre. 1989. Esters caféiques de deux verbénacées des Antilles. Plantes Médicinales et Phytothérapie 23: 1–5.

Gentry, A. H. 1976. Bignoniaceae of southern Central America: Distribution and ecological specificity. Biotropica 8: 117–131.

Gibson, D. N. 1970. Verbenaceae of Guatemala. *In:* P. C. Standley & L. O. Williams (editors), Flora of Guatemala. Fieldiana, Bot. 24: 192–195.

Goldblatt, P. 1988. Index to Plant Chromosome Numbers 1984–1985. Monogr. Syst. Bot. Missouri Bot. Gard. 23: 214.

Hewson, H. J. 1988. Plant Indumentum: A Handbook of Terminology. Australian Government Publishing Service, Canberra.

Hickey, L. J. 1979. A revised classification of the architecture of dicotyledonous leaves. Pp. 25–39 *in* C. Metcalfe & L. Chalk (editors), Anatomy of the

Dicotyledons, 2nd ed., Vol. 1. Clarendon Press, Oxford.

HUMBOLDT, F. H. A., A. J. BONPLAND & C. S. KUNTH. 1818. Nova Genera et Species Plantarum. Vol. 2: 282. Lutetiae Parisiorum, Paris.

JANSEN-JACOBS, M. J. 1988. Verbenaceae. *In:* A. R. A. Görts-van Rijn, editor, Flora of Guianas. Koeltz Scientific Books, Koenigstein.

JANZEN, D. H. 1971. Escape in space by *Sterculia apetala* seeds from the bug *Dysdercus fasciata* in a Costa Rican deciduous forest. Ecology 53: 350–361.

JOHANSEN, D. 1940. Plant Microtechnique. McGraw-Hill, New York.

JUNNEL, S. 1934. Zur Gynäceummorphologie und Systematik der Verbenaceen und Labiaten. Symb. Bot. Upsal. 4: 1–219.

KAPLAN, D. 1984. The concept of homology and its central role in the elucidation of plant systematic relationships. Pp. 51–70 *in* T. F. Steussy & T. Duncan (editors), Cladistics: Perspectives on the Reconstruction of Evolutionary History. Columbia Univ. Press, New York.

LINNAEUS, C. 1737. Genera Plantarum, ed. 1: 347. Lugduni Batavorum, Leiden.

———. 1753. Species Plantarum. Vol. 2: 626. Laurentii Salvii, Stockholm.

MACBRIDE, J. F. 1960. Flora of Peru: Verbenaceae. Publ. Field Mus. Nat. Hist. Bot. Ser. 13: 609–720.

MADDISON, W. P., M. J. DONOGHUE & D. R. MADDISON. 1984. Outgroup analysis and parsimony. Syst. Zool. 33: 83–103.

METCALFE, C. R. & L. CHALK. 1972. Anatomy of the Dicotyledons. Clarendon Press, Oxford.

——— & ———. 1979. Anatomy of the Dicotyledons, 2nd ed., Vol. 1. Clarendon Press, Oxford.

MOLDENKE, H. N. 1938. A monograph of the genus *Petrea*. Feddes Rep. 43: 1–48, 161–221.

———. 1971. A Fifth Summary of the Verbenaceae, Avicenniaceae, Stilbaceae, Dicrastylidaceae, Symphoremaceae, Nyctanthaceae, and Eriocaulaceae of the world as to Valid Taxa, Geographic Distribution, and Synonymy. Published by the author.

———. 1973. Verbenaceae of Panama. *In:* R. E. Woodson & R. W. Schery (editors), Flora of Panama. Ann. Missouri. Bot. Gard. 60: 137–144.

NIXON, K. C. 1992. Clados version 1.1. IBM PC-compatible character analysis program. Documentation published by the author. Cornell University, Ithaca.

PAYNE, W. W. 1978. A glossary of plant hair terminology. Brittonia 30: 239–255.

PITTIER, H. 1925. Arboles y arbustos nuevos de Venezuela. Bol. Ci. Técn. Mus. Comercial Venezuela. 1: 70.

PUFF, C. 1978. The peculiar trichomes of *Petrea volubilis* (Verbenaceae). J. S. African Bot. 44: 119–125.

PUTZ, F. E. 1982. Natural History of Lianas and their Influences on Tropical Forest Dynamics. Unpublished Ph.D. thesis. Cornell University, Ithaca, New York.

RECORD, S. J. & R. W. HESS. 1941. American woods of the family Verbenaceae. Trop. Wood 65: 4–21.

RUEDA, R. M. 1992. A new species of *Petrea* (Verbenaceae) from Brazilian Amazonia. Novon 2: 417–418.

———. 1993. Lectotypifications in the genus *Petrea* (Verbenaceae). Novon 3: 179–181.

SCHAUER, J. C. 1847. Verbenaceae. *In:* A. L. P. Candolle, Prodromus Systematis Naturalis Regni Vegetalis 11: 616–621.

SHARMAN, B. 1943. Tannic acid and iron alum with safranin and orange G in studies of the shoot apex. Stain Technol. 18: 105–111.

SINCLAIR, C. B. & D. B. DUNN. 1961. Surface printing of plant leaves for phylogenetic studies. Stain Technol. 36: 299–304.

STAFLEU, F. A. & R. COWAN. 1979. Taxonomic Literature, 2nd ed. Bohn, Scheltema & Holkema, Utrecht.

WATROUS, L. & Q. WHEELER. 1981. The out-group comparison method of character analysis. Syst. Zool. 30: 1–11.

WELLE, B. J. H. & P. DETIENNE. 1988. Wood and timber of Verbenaceae. Pp. 87–99 *in* A. R. A. Görts-van Rijn, editor, Flora of Guianas. Koeltz Scientific Books, Koenigstein.

WILBERT, W. & D. NEILL. 1987. Medical Ethnobotany of the Quijos-Quichua of the upper Río Napo, Amazonian Ecuador. Published by the authors.

LIST OF EXSICCATAE. Numbers in parentheses correspond to species as numbered in the text.

Acevedo, P., 4239 (11); 4840 (2). Acosta, R., 245 (11). Aguilar, J. A., 130 (11). Aguilar, J. I., 1212 (11). Aguilar, M., 362 (11). Alcorn, J. B., 2451A, 2920A, 2013, 3527 (11). Allard, H. A., 13175, 14534 (11). Allen, P. H., 960, 4293, 5733, 6272 (11). Almeda, F., 4077 (11). Almeida, S. S., 213, 229 (2). Alston, A. H., 5976 (11). Alvarado, F., 187 (11). Amaral, I. L., 446 (11). Amaral, J., 3 (11). Ancuash, E., 1388 (7). Anderson, A., 229 (5). Anderson, E., 5232 (11). Anderson, C. W., *s.n.* (11). Andrade, A. G., 951 (11). Andrade, J. B., 3292 (7). André, E. F., 4707 (8). Antonio, T. M., 4247, 4621 (11). Apollinaire, Bro., *s.n.* (11). Appun, C., *s.n.* (9). Araquistain, M., 3786 (11). Archer, W. A., 3358 (9). Argeñal, F. J., 67 (11). Arias, L. M., 86 (11). Aristeguieta, L., 1602, 3463, 4113, 4674 (8). Arnason, T., 17046 (11). Arnoldo, U., 1052, 1363 (11). Artamanoff, G., 193 (11). Atkinson, D. J., 4, 17 (2). Aviles, S., 14 (11). Ayala, F., 2894, 4509 (1). Aymard, G., 99, 1864, 1865, 2585, 4446, 6569 (8), 336, 998, 2529, 8888, 8889 (11).

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Wachenheim, M., 5, 249 (2). Wagner, M., 586 (11). Wagner, R. J., 786 (11). Walker, E. H., 8074 (11). Walker, R. L., 1229 (11). Warren, L. B., *s.n.* (11). Wasshausen, D., 357 (11). Watdahnahsahp, B., 70 (11). Webster, G. L., 9086 (11). Weitzman, A., 243 (11). Welch, W. H., 9667 (11). Wendt, T., 122 (11). Werff, H. van der, 9823 (1); 10417 (8). Wetmore, R. H., 162

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SYSTEMATIC IMPLICATIONS OF POLLEN MORPHOLOGY IN SUBFAMILIES LAMIOIDEAE AND POGOSTEMONOIDEAE (LABIATAE)[1]

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Abstract

Pollen morphology was surveyed in 57 of the 60 genera of Lamioideae and Pogostemonoideae sensu Cantino et al. and two genera of uncertain subfamilial affinities: *Anisomeles* and *Eurysolen*. Pollen in all Pogostemonoideae, most Lamioideae, *Anisomeles*, and *Eurysolen* is tricolpate with suprareticulate sculpturing. Variants found in a few genera of Lamioideae include tetracolpate and hexapantocolpate pollen and psilate, granulate, and rugulate sculpturing. Most species in which pollen was examined in section have simple columellae, but seemingly branched columellae were observed in *Gomphostemma*, *Chelonopsis*, and one species of *Stenogyne*. With regard to the genera of uncertain affinities, the findings presented here support a relationship between *Anisomeles* and *Pogostemon*; the position of *Eurysolen* remains unclear. Within subfamily Lamioideae, pollen morphology supports the segregation of *Lamiophlomis*, *Lagopsis*, and *Phlomidoschema* from *Phlomis*, *Marrubium*, and *Stachys*, respectively. Hexapantocolpate pollen is hypothesized to be a synapomorphy of *Sideritis* section *Empedoclea*. Similarities in pollen sculpturing were noted between *Brazoria*, *Macbridea*, and *Physostegia*, and between *Galeopsis* and *Synandra*.

A pollen survey of subfamily Lamioideae sensu Erdtman (1945) was undertaken with the hope that it might further our understanding of systematic relationships. A brief overview of the study as a whole has been published (Abu-Asab & Cantino, 1992), with elaboration elsewhere on two small subgroups that appear not to be closely related to the remainder of the study group (Abu-Asab & Cantino, 1993a, b). It is our intent here to document in detail the pollen morphology of the bulk of Erdtman's Lamioideae—i.e., those genera with a gynobasic style.

A taxonomic clarification is needed because we have circumscribed subfamily Lamioideae differently here than in some of our earlier works (e.g., Cantino & Sanders, 1986; Abu-Asab, 1990; Cantino, 1990, 1992a; Abu-Asab & Cantino, 1992). Although the pollen survey was initiated as a study of the Lamioideae sensu Erdtman (1945), and our earlier papers adopted Erdtman's circumscription, recent evidence that this taxon is polyphyletic (Abu-Asab & Cantino, 1992; Cantino, 1992b) led to an alternative classification (Cantino et al., 1992), which is followed here. Unless otherwise indicated, all references herein to subfamily Lamioideae imply the circumscription of Cantino et al. (1992).

Subfamily Lamioideae comprises 55 genera, the vast majority of them Eurasian (Table 1). Subfamily Pogostemonoideae is an Asian group of five genera. Based on morphological and molecular evidence, the two subfamilies are closely related (Cantino, 1992a; Downie & Palmer, 1992), and *Eurysolen* resembles genera in both. (See Table 1 for authors of genus names and Appendix for authors of species names.) *Anisomeles* has been variably assigned to both subfamilies (see Discussion).

Most pollen studies that included members of Lamioideae and Pogostemonoideae have centered on particular genera (e.g., Huynh, 1972; Bassett & Munro, 1986) or geographical regions (e.g., Waterman, 1960; Varghese & Verma, 1968; Huang, 1972). Risch (1956) and Pozhidaev (1989) conducted broader surveys of the Labiatae, but Risch used only light microscopy, and his descrip-

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TABLE 1. Genera of Lamioideae and Pogostemonoideae. Numbers in parentheses: number of species in the genus/number of species studied (Appendix). Numbers of species were taken from a variety of sources, geographic distributions mostly from Mabberley (1987) and Airy Shaw (1973).

Subfamily Lamioideae

Achyrospermum Blume (10/6)—Paleotropics
Acrotome Benth. ex Endl. (8/4)—Tropical & southern Africa
Ajugoides Makino (1/1)—Japan
Alajja Ikonn. (1/1)—Himalayas
Ballota L. (35/7)—Europe, Africa, western Asia
Bostrychanthera Benth. (1/0)—China
Brazoria Engelm. & A. Gray (4/4)—Texas, Oklahoma
Chaiturus Willd. (1/1) –Temperate Eurasia
Chamaesphacos Schrenk ex Fischer & C Meyer (1/1)—Central & southwestern Asia
Chelonopsis Miq. (13/2)—Himalayas, China, Japan
Colquhounia Wallich (5/2)—Himalayas
Craniotome Rchb. (1/1)—Himalayas
Eremostachys Bunge ex Ledeb. sensu lato (60/4)—Europe to central Asia
Eriophyton Benth. (1/1)—Himalayas
Galeopsis L. (10/6)—Temperate Eurasia
Gomphostemma Wallich ex Benth. (30/7)—Southeastern Asia, Malesia
Haplostachys (A. Gray) Hillebrand (5/2)—Hawaii
Hypogomphia Bunge (1/1)—Central & southwestern Asia
Isoleucas Schwartz (1/0)—Arabia
Lagochilus Bunge ex Benth. (35/3)—Central & southwestern Asia
Lagopsis Bunge (4/2)—Western Siberia to Japan
Lamiophlomis Kudo (1/1)—Himalayas
Lamium L. (16/7)—Temperate Eurasia, northern Africa
Leonotis (Pers.) R. Br. (15/3)—Tropical & southern Africa, 1 pantropical
Leonurus L. (24/2)—Temperate Eurasia
Leucas R. Br. (100/17)—Pantropical, southern Africa, China
Loxocalyx Hemsley (3/2)—China, Japan
Macbridea Elliott ex Nutt. (2/2)—Southeastern United States
Marrubium L. (30/5) –Europe, northern Africa, central & southwestern Asia
Melittis L. (1/1)—Europe
Metastachydium Airy Shaw ex C. Y. Wu & Li (1/1)—Central Asia
Microtoena Prain (25/4)—Himalayas, China
Moluccella L. (2/2) –Southern Europe, southwestern Asia
Notochaete Benth. (1/1)—Himalayas
Otostegia Benth. (20/5)– Northeastern tropical Africa to central Asia
Panzerina Soják (2/1)—Western Siberia to Mongolia
Paralamium Dunn (1/1)—Southwestern China
Paraphlomis Prain (8/3)—Eastern Asia, Malesia
Phlomidoschema (Benth.) Vved. (1/1)—Iran to western Himalayas
Phlomis L. (ca. 100/7)—Mediterranean region to China
Phyllostegia Benth. (28/5)—Hawaii, Tahiti
Physostegia Benth. (12/2)—North America
Prasium L. (1/1)—Mediterranean region
Pseuderemostachys Popov (1/1)—Central Asia
Pseudomarrubium Popov (1/0)—Central Asia
Roylea Wallich ex Benth. (1/1)—Himalayas
Sideritis L. (ca. 130/19)—Mediterranean region to southwestern Asia, Macaronesia
Stachyopsis Popov & Vved. (3/1)—Central Asia to western China
Stachys L. (ca. 300/2)—Northern & southern temperate & subtropical; tropical mountains
Stenogyne Benth. (20/3)—Hawaii
Sulaimania Hedge & Rech. f. (1/1)—Pakistan
Suzukia Kudo (2/1)—Taiwan, Ryukyus
Synandra Nutt. (1/1)—Eastern United States
Thuspeinanta T. Durand (2/1)—Central & southwestern Asia
Weidemannia Fischer & C. Meyer (2/1)—Southwestern Asia

Subfamily Pogostemonoideae

Colebrookea Smith (1/1)—India
Comanthosphace S. Moore (7/3)—Eastern Asia
Leucosceptrum Smith (1/1)—Himalayas, China
Pogostemon Desf. (71/10) –China, India, Malesia
Rostrinucula Kudo (2/1)—Eastern Asia

Genera of uncertain affinities

Anisomeles R. Br. (6/4)—Paleotropics
Eurysolen Prain (1/1)—Southeastern Asia, Indomalesia

TABLE 1. Continued.

tions emphasized gross pollen morphology (i.e., size, shape, color). Pozhidaev's (1989) survey used scanning electron microscopy (SEM), but the resulting publication focused on variation in exine structure in the family as a whole; the pollen morphology of individual genera was not systematically described, and micrographs were provided for less than a third of the genera studied. We are aware of published SEM pollen micrographs for only 25 of the 60 genera of Lamioideae and Pogostemonoideae (Nabli, 1976; Roca Salinas, 1978; Azizian & Moore, 1982; Cantino, 1982; Ubera & Galán, 1983; Bassett & Munro, 1986; Cantino & Sanders, 1986; Pozhidaev, 1989, 1992; Abu-Asab & Cantino, 1992; Demissew & Harley, 1992; Trudel & Morton, 1992). Few species have been studied, so the degree of intrageneric variation in surface sculpturing is unknown for most of these genera;

exceptions are *Eremostachys*, *Paraphlomis*, *Phlomis*, *Physostegia*, and *Stachys*. Transmission electron microscope (TEM) photographs have been published for only three genera (Nabli, 1976; Abu-Asab & Cantino, 1992).

The objectives of this paper are to document the pollen morphology of subfamilies Lamioideae and Pogostemonoideae, including interspecific variation within most of the larger genera, and to evaluate the systematic significance of the resulting data. Because the resulting compilation of SEM photographs includes nearly every genus in these subfamilies, it should serve as a useful reference for those studying the systematics or palynology of the Labiatae.

Materials and Methods

The study collection (Table 1) comprised 183 species representing all five genera of Pogostemonoideae, 52 of the 55 genera of Lamioideae, and two genera of uncertain subfamilial affinities (*Anisomeles* and *Eurysolen*). In most of the larger genera, an effort was made to sample a broad spectrum of species by reference to the infrageneric classifications of Briquet (1895–1897) and available monographs and revisions. *Eremostachys*, *Phlomis*, *Physostegia*, and *Stachys* were only superficially sampled because they have already received considerable study (Azizian & Moore, 1982; Cantino, 1982; Ubera & Galán, 1983; Bassett & Munro, 1986; Demissew & Harley, 1992). The monotypic genera *Bostrychanthera*, *Pseudomarrubium*, and *Isoleucas* were not examined for lack of material, but micrographs of the former two were provided by Pozhidaev (1989); thus only the pollen of *Isoleucas* remains totally unknown.

Pollen obtained from mature buds (vouchers listed in Appendix) was prepared for SEM, TEM, and light microscopy (LM) using the prolonged acetolysis procedure of Abu-Asab & Cantino (1989), modified from Erdtman (1960). For LM, including size measurements, the pollen was mounted in glycerine jelly and sealed with paraffin. In most cases, seven to ten grains were measured per species. The ratio of polar to equatorial axis length (P/E) was determined for each measured grain, and the mean P/E ratio was calculated from these individual values. For SEM, pollen was coated with gold-palladium and examined and photographed with a Hitachi HHS-2R scanning electron microscope. For TEM, pollen was treated with osmium tetroxide, stained with uranyl acetate, and embedded in resin. Thin sections were collected on carbon-stabilized Formvar, stained with aqueous uranyl acetate and lead citrate, and examined and photographed with a Hitachi HS-8 transmission electron microscope.

Results

The results are summarized in Table 2, and representative pollen grains are illustrated in Figures 1–247. The distinction between foveolate, microreticulate, punctate, reticulate, and scrobiculate sculpturing follows Vezey et al. (1992), a more precise system of terminology than used in our previous papers (Abu-Asab, 1990; Abu-Asab & Cantino, 1989, 1992, 1993a, b; Abu-Asab et al., 1993). Pollen that we previously referred to as tectate-perforate is described here as scrobiculate or punctate.

LAMIOIDEAE

Pollen of subfamily Lamioideae is suboblate to euprolate (shape classification follows Walker & Doyle, 1975, based on P/E ratios in Table 2), with the polar axis 15–59 μm and the equatorial axis 13–52 μm. The grains are inoperculate and usually tricolpate; tetracolpate and hexapantocolpate grains were found in a few genera (Table 2). The exine in most species is scrobiculate (sometimes bordering on microreticulate or punctate). The exine is microreticulate in seven species, reticulate in one, and partially foveolate in one (Table 2). The sculpturing is suprareticulate in most species (referred to as bi-reticulate by some authors; Demissew & Harley, 1992; Harley et al., 1992), but four other forms of sculpturing were found: psilate, granulate, rugulate, and suprareticulate-rugulate. The columellae are usually simple but sparsely branched in a few species.

The pollen features in a few genera warrant a more detailed description than is available in Table 2:

Gomphostemma (Figs. 62–76; Pozhidaev, 1989): sculpturing exceptionally variable: psilate or with suprareticulate, rugulate, or granulate sculpturing; columellae branched.

Lagopsis (Fig. 77): exine rugulate, psilate toward the poles, apparently nonperforate.

Sideritis (Figs. 182–196; Huynh, 1972; Nabli, 1976; Roca Salinas, 1978; Pozhidaev, 1992): tetracolpate (the amb circular to more or less square), 6-pantocolpate (the amb circular), or rarely tricolpate (the amb triangular); exine psilate (approaching a suprareticulate condition in section *Empedoclea* (Raf.) Benth.; Figs. 192, 193), usually scrobiculate (in *S. montana*, the polar regions and centers of the three mesocolpia foveolate, the

TABLE 2. Summary of pollen morphological data for subfamilies Lamioideae and Pogostemonoideae and genera of uncertain affinities. Colpi: 3, tricolpate; 4, tetracolpate; 6, hexapantocolpate. Columellae: simple vs. branched. Sculpturing: Upper layer: Gr, granulate; Ps, psilate; Ru, rugulate; Sr, suprareticulate-rugulate; Su, suprareticulate. Lower layer (or only layer if psilate): Fo, foveolate; Mi, microreticulate; Np, nonperforate; Pu, punctate; Re, reticulate; Sc, scrobiculate; slash indicates borderline designations.

Species	Polar axis (μm)		Equatorial axis (μm)		P/E ratio		Colpi	Columellae	Sculpturing		Figures
	Mean	Range	Mean	Range	Mean	Range			Upper	Lower	
Subfamily Lamioideae											
Achyrospermum aethiopicum	21.3	(20–22)	18.5	(18–20)	1.16	(1.0–1.3)	3		Su	Sc	1, 2
Achyrospermum carvalhi	26.9	(22–31)	23.9	(20–29)	1.13	(0.8–1.3)	3		Su	Sc/Mi	3
Achyrospermum cryptanthum	24.0	(22–31)	19.1	(18–22)	1.25	(1.1–1.4)	3		Su	Sc	4
Achyrospermum densiflorum	24.5	(22–26)	18.4	(15–22)	1.34	(1.0–1.7)	3		Su	Sc	5
Achyrospermum parviflorum	23.3	(22–24)	18.9	(18–20)	1.24	(1.1–1.3)	3		Su	Sc	6, 7
Achyrospermum schimperi	28.0	(22–33)	20.9	(20–22)	1.34	(1.1–1.5)	3		Su	Sc	8, 9
Acrotome angustifolia	20.2	(20–22)	18.0	(17–20)	1.13	(1.0–1.3)	3		Su	Sc	10, 11
Acrotome fleckii	20.7	(20–22)	22.0	(20–24)	0.94	(0.8–1.1)	3		?	?	
Acrotome hispida	20.0	(—)	21.6	(20–22)	0.92	(0.9–1.0)	3		?	?	
Acrotome inflata	22.9	(22–24)	22.9	(22–24)	1.00	(0.9–1.1)	3		?	?	
Ajugoides humilis	31.9	(31–35)	23.5	(22–26)	1.36	(1.2–1.6)	3		Su	Sc/Mi	12, 13
Alajja rhomboidea	30.1	(29–33)	28.4	(26–31)	1.06	(0.9–1.3)	3		Su	Sc	14, 15
Ballota africana	22.7	(22–24)	20.7	(20–22)	1.10	(1.0–1.2)	3		Su	Sc	16
Ballota andreuzziana	23.5	(22–24)	20.9	(20–22)	1.13	(1.0–1.2)	3		Su	Sc/Mi	
Ballota hirsuta	22.0	(—)	18.0	(17–20)	1.22	(1.1–1.3)	3		Su	Sc	17, 18
Ballota integrifolia	21.6	(20–24)	21.3	(20–24)	1.01	(0.9–1.1)	3		Su	Mi	19
Ballota nigra	23.8	(22–26)	20.9	(18–24)	1.14	(1.0–1.3)	3		Su	Sc	20
Ballota pseudodictamnus	29.3	(26–31)	20.5	(18–22)	1.43	(1.3–1.6)	3		Su	Sc/Mi	21, 22
Ballota rupestris	21.2	(20–22)	23.4	(22–24)	0.90	(—)	3		Su	Sc	
Brazoria arenaria	35.2	(33–40)	32.3	(31–33)	1.09	(1.0–1.2)	3		Su	Sc	23
Brazoria pulcherrima	37.0	(35–42)	31.7	(29–33)	1.17	(1.1–1.5)	3		Su	Sc	24
Brazoria scutellarioides	32.5	(29–35)	33.0	(29–35)	0.99	(0.8–1.2)	3		Su	?	25
Brazoria truncata	39.2	(37–42)	32.6	(29–35)	1.21	(1.1–1.5)	3		Su	Sc	26, 27
Chaiturus marrubiastrum	21.2	(20–23)	20.5	(18–22)	1.04	(0.9–1.2)	3		Su	Sc	28, 29
Chamaesphacos ilicifolius	30.4	(24–33)	24.0	(20–26)	1.27	(1.1–1.4)	3		Su	Sc	30
Chelonopsis lichiangensis	28.4	(24–31)	27.3	(24–31)	1.04	(0.9–1.2)	3	Branched?	Su	Sc/Mi	31, 32
Chelonopsis odontochila	28.0	(26–29)	26.4	(24–29)	1.06	(1.0–1.2)	3		Su	Sc/Mi	33, 34
Colquhounia coccinea	27.7	(26–31)	26.6	(26–29)	1.04	(0.9–1.2)	3		Su	Sc	
Colquhounia seguinii	23.3	(22–26)	21.6	(20–24)	1.09	(0.9–1.3)	3		Su	Sc	35, 36
Craniotome furcata	16.6	(15–18)	14.9	(13–15)	1.12	(1.0–1.3)	3		Su	Sc	37–39
Eremostachys fetissovii	33.4	(31–37)	29.5	(24–33)	1.14	(0.9–1.6)	3		Su	Sc	
Eremostachys iliensis	31.7	(31–33)	27.1	(24–29)	1.17	(1.1–1.3)	3		Su	Sc	40, 41

TABLE 2. Continued.

Species	Polar axis (μm) Mean	Polar axis (μm) Range	Equatorial axis (μm) Mean	Equatorial axis (μm) Range	P/E ratio Mean	P/E ratio Range	Colpi	Columellae	Sculpturing Upper	Sculpturing Lower	Figures
Eremostachys rotata	34.5	(29–37)	32.3	(29–35)	1.07	(0.8–1.2)	3		Su	Sc	42
Eremostachys speciosa	35.9	(33–37)	29.5	(26–33)	1.23	(1.1–1.4)	3		Su	Sc	43
Eriophyton wallichianum	28.6	(26–31)	23.5	(22–26)	1.22	(1.0–1.4)	3		Su	Sc	44, 45
Galeopsis bifida	38.7	(33–46)	32.1	(26–37)	1.22	(0.9–1.4)	3		Su	Sc	46, 47
Galeopsis ladanum	34.9	(31–40)	26.7	(24–31)	1.31	(1.2–1.5)	3		Su	Sc	
Galeopsis pubescens	32.1	(26–35)	26.0	(22–31)	1.24	(1.0–1.4)	3		Su	Sc	48
Galeopsis segetum	35.2	(31–40)	26.8	(24–31)	1.32	(1.0–1.6)	3		Su	?	
Galeopsis speciosa	37.8	(35–40)	27.3	(26–29)	1.39	(1.2–1.5)	3		Su	Sc	49
Galeopsis tetrahit	38.5	(35–42)	29.0	(26–31)	1.33	(1.1–1.5)	3		Su	Sc	50
Gomphostemma chinense	33.7	(31–35)	33.4	(33–35)	1.01	(0.9–1.1)	3		Gr	Sc/Mi	62, 63
Gomphostemma intermedium	32.1	(31–35)	32.6	(31–33)	0.99	(0.9–1.0)	3	Branched	Ps	Mi	64–66
Gomphostemma javanicum	29.7	(26–31)	30.8	(29–33)	0.97	(0.9–1.0)	3		Ru	Sc	69, 70
Gomphostemma leptodon	33.2	(29–40)	35.4	(29–42)	0.94	(0.9–1.2)	3		Ps	Sc	67, 68
Gomphostemma lucidum	32.3	(29–37)	32.6	(31–33)	0.99	(0.8–1.1)	3	Branched	Ps	Sc	71, 72
Gomphostemma parviflorum	26.6	(24–29)	25.7	(24–29)	1.04	(0.9–1.1)	3		Gr	Sc	73, 74
Gomphostemma wallichii	29.9	(29–31)	31.7	(31–33)	0.95	(0.9–1.0)	3		Su	Sc	75, 76
Haplostachys haplostachya	51.0	(44–57)	48.4	(46–51)	1.06	(0.9–1.2)	3, 4		Su	Sc	51, 52
Haplostachys linearifolia	49.7	(46–55)	46.2	(44–48)	1.08	(1.0–1.2)	3, 4		Su	Sc	53, 54
Hypogomphia turkestana	33.4	(29–40)	27.4	(24–29)	1.22	(1.0–1.5)	3	Simple	Su	Sc	55–57
Lagochilus aucheri	25.5	(24–26)	24.2	(22–26)	1.06	(1.0–1.2)	3		Su	?	58, 59
Lagochilus diacanthophyllus	28.2	(26–29)	22.7	(20–24)	1.25	(1.1–1.4)	3		Su	Sc	60, 61
Lagochilus hirtus	25.5	(22–29)	21.1	(20–24)	1.22	(0.9–1.3)	3		Su	Sc	
Lagopsis marrubiastrum	21.2	(20–23)	19.6	(18–21)	1.08	(0.9–1.2)	3		Ru+Ps	Np?	77
Lagopsis supina	21.1	(20–22)	21.8	(20–24)	0.97	(0.9–1.1)	3		?	?	
Lamiophlomis rotata	24.2	(22–26)	20.0	(18–22)	1.21	(1.1–1.3)	3		Ps	Sc	78, 79
Lamium album	25.1	(22–29)	23.8	(22–26)	1.06	(0.8–1.3)	3		Gr	Sc	80, 81
Lamium flexuosum	23.5	(22–26)	21.8	(18–24)	1.09	(0.9–1.3)	3	Simple	Su	Sc	82, 83
Lamium galeobdolon	30.8	(29–33)	22.9	(20–26)	1.36	(1.1–1.6)	3		Su	Sc	86, 87
Lamium garganicum	28.6	(26–33)	26.8	(24–29)	1.07	(1.0–1.2)	3	Simple	Su	Mi	84, 85
Lamium moluccellifolium	34.1	(33–35)	30.1	(26–33)	1.14	(1.0–1.3)	3		Su	?	
Lamium moschatum	21.2	(20–22)	20.6	(20–22)	1.03	(0.9–1.1)	3		Gr	Sc	88, 89
Lamium purpureum							3		Su	Sc	90, 91
Leonotis bequaertii	30.7	(29–33)	29.9	(28–33)	1.02	(0.8–1.2)	3		Su	Sc	92, 93
Leonotis leonitis	28.6	(26–31)	24.9	(24–26)	1.15	(1.1–1.3)	3	Simple	Su	Sc	94–96
Leonotis mollissima	31.9	(29–35)	28.6	(22–33)	1.13	(0.9–1.5)	3	Simple	Su	Sc	97

TABLE 2. Continued.

Species	Polar axis (μm)		Equatorial axis (μm)		P/E ratio		Colpi	Columellae	Sculpturing		Figures
	Mean	Range	Mean	Range	Mean	Range			Upper	Lower	
Leonurus cardiaca	22.7	(22–24)	21.1	(20–24)	1.08	(1.0–1.1)	3		Su	Sc	98, 99
Leonurus sibiricus	25.5	(22–29)	21.3	(20–24)	1.20	(1.0–1.4)	3		Su	Sc	100
Leucas abyssinica	20.5	(18–22)	19.1	(18–20)	1.07	(1.0–1.1)	3		Su	Sc	107, 108
Leucas alluaudii	26.0	(22–31)	22.9	(20–26)	1.14	(1.0–1.4)	3		Su	Sc	109
Leucas aspera	24.0	(22–26)	19.6	(18–22)	1.23	(1.1–1.4)	3		Su	Sc/Mi	110, 111
Leucas biflora	29.3	(26–31)	23.1	(22–26)	1.27	(1.1–1.4)	3		Su	Sc	
Leucas calostachys	25.3	(24–26)	22.4	(20–24)	1.14	(1.0–1.3)	3		Su	Sc	112, 113
Leucas ciliata	23.3	(22–24)	22.7	(22–24)	1.03	(0.9–1.1)	3		Su	Sc	
Leucas eriostoma	20.9	(20–22)	17.6	(15–20)	1.20	(1.1–1.4)	3		Su	Mi	114
Leucas hirta	20.5	(20–22)	16.7	(15–20)	1.24	(1.0–1.4)	3		Su	Sc	115
Leucas inflata	20.0	(—)	18.1	(17–20)	1.10	(1.0–1.1)	3		Su?	?	116
Leucas javanica	26.4	(22–31)	24.2	(22–26)	1.09	(0.9–1.3)	3		Su	Sc/Mi	117
Leucas lanata	27.3	(26–29)	20.5	(18–22)	1.34	(1.2–1.5)	3		Su	Sc	
Leucas lavandulifolia	26.4	(24–29)	22.7	(20–24)	1.17	(1.1–1.3)	3		Su	Sc	
Leucas marrubioides	22.9	(20–24)	17.8	(15–20)	1.29	(1.0–1.4)	3		?	?	
Leucas martinicensis	22.6	(22–24)	20.1	(19–22)	1.13	(1.0–1.2)	3		Su	Sc	
Leucas mollissima	29.6	(29–31)	23.0	(22–24)	1.29	(1.2–1.4)	3		?	?	
Leucas rosmarinifolia	22.2	(20–24)	18.5	(18–20)	1.21	(1.1–1.4)	3	Simple	Su	?	118
Leucas stelligera	21.1	(20–24)	18.9	(18–20)	1.12	(1.0–1.3)	3		Su	Sc	
Loxocalyx ambiguus	23.8	(22–26)	21.3	(20–22)	1.12	(1.0–1.3)	3		Su	Sc/Mi	101
Loxocalyx urticifolius	24.0	(22–26)	20.9	(20–24)	1.16	(0.9–1.3)	3		Su	Sc	102, 103
Macbridea alba	47.3	(42–53)	34.5	(31–37)	1.37	(1.2–1.5)	3		Su	Sc	104
Macbridea caroliniana	38.1	(35–42)	40.5	(40–42)	0.94	(0.9–1.1)	3		Su	Sc	105, 106
Marrubium anisodon	27.5	(24–31)	29.0	(26–31)	0.95	(0.8–1.1)	4		Ps	Sc	122, 123
Marrubium cuneatum	24.9	(24–26)	26.8	(24–29)	0.93	(0.8–1.1)	3		Ps	Sc	
Marrubium heterodon	26.4	(24–29)	27.7	(26–29)	0.95	(0.8–1.1)	3		Ps	Sc/Pu	124, 125
Marrubium incanum	52.3	(51–55)	46.9	(44–51)	1.12	(1.1–1.2)	3		Ps	Sc/Pu	
Marrubium supinum	24.0	(—)	25.9	(24–26)	0.93	(0.9–1.0)	3	Simple	Ps	Sc	126–128
Melittis melissophyllum	45.8	(40–51)	35.6	(31–40)	1.29	(1.2–1.5)	3		Su	Sc	119, 120
Metastachydium sagittatum	22.2	(22–24)	23.1	(22–24)	0.96	(0.9–1.1)	3		Su	Sc	121
Microtoena delavayi							3	Simple	Su	Sc/Mi	129–131
Microtoena insuavis							3		Su	Mi	132
Microtoena robusta	32.8	(29–37)	28.8	(24–33)	1.15	(0.9–1.4)	3		Su	Mi	133, 134
Microtoena urticifolia	24.6	(22–26)	28.2	(24–31)	0.88	(0.8–0.9)	3		Su	Mi	135, 136
Moluccella laevis	34.8	(33–40)	28.2	(26–31)	1.24	(1.1–1.5)	3		Su	Sc/Mi	137

TABLE 2. Continued.

Species	Polar axis (μm)		Equatorial axis (μm)		P/E ratio		Colpi	Columellae	Sculpturing		Figures
	Mean	Range	Mean	Range	Mean	Range			Upper	Lower	
Moluccella spinosa	29.5	(29–31)	30.4	(29–31)	0.97	(0.9–1.1)	3		Su	Sc	138, 139
Notochaete hamosa	30.1	(26–33)	29.3	(26–31)	1.03	(0.8–1.2)	3		Ps	Sc	140, 141
Otostegia fruticosa	21.8	(20–22)	21	(20–22)	1.04	(1.0–1.1)	3		Su	Sc	142, 143
Otostegia integrifolia	29.0	(26–33)	23.8	(22–26)	1.23	(1.0–1.4)	3		Su	Sc/Mi	144
Otostegia minuccii	24.2	(22–26)	21.1	(20–22)	1.15	(1.0–1.2)	3		Su	Sc	
Otostegia repanda	20.9	(20–22)	17.2	(15–18)	1.22	(1.1–1.4)	3		Su	Sc	145
Otostegia tomentosa	21.1	(18–22)	18.3	(18–20)	1.16	(1.0–1.3)	3	Simple	Su	Sc	146, 147
Panzerina lanata	23.3	(22–26)	19.4	(18–22)	1.21	(1.0–1.5)	3		Su	Sc	148–150
Paralamium gracile	16.3	(15–20)	15.0	(13–18)	1.10	(0.9–1.5)	3		Su	Sc	151
Paraphlomis javanica	30.1	(29–33)	32.8	(29–35)	0.92	(0.8–1.0)	3		Sr	Sc	152, 153
Paraphlomis lanceolata	26.8	(26–29)	26.0	(24–29)	1.04	(1.0–1.2)	3		Su	Sc/Mi	154, 155
Paraphlomis rugosa	30.0	(26–37)	31.2	(29–37)	0.96	(0.8–1.1)	3		Su	Sc	156
Phlomidoschema parviflorum	24.2	(22–26)	21.6	(18–26)	1.14	(1.0–1.4)	3		Ps	Sc	157, 158
Phlomis agraria	29.5	(29–31)	25.7	(24–29)	1.15	(1.0–1.3)	3		Su	Sc	159, 160
Phlomis crinita	33.9	(33–35)	25.1	(22–26)	1.36	(1.3–1.5)	3		Su	?	
Phlomis herba-venti	34.1	(31–37)	28.4	(26–31)	1.20	(1.1–1.4)	3		?	?	
Phlomis lanata	40.3	(37–44)	29.0	(26–33)	1.39	(1.2–1.6)	3		Su	Sc	161, 162
Phlomis maximoviczii	20.9	(20–22)	18.9	(18–20)	1.11	(1.0–1.3)	3		Gr	Sc	163
Phlomis tuberosa	27.3	(24–29)	25.5	(24–26)	1.07	(1.0–1.2)	3		Su	Sc	164
Phlomis umbrosa	19.6	(18–22)	16.1	(15–18)	1.22	(1.1–1.3)	3		Gr	Sc/Mi	165, 166
Phyllostegia grandiflora	42.5	(40–44)	45.8	(44–48)	0.93	(0.8–1.0)	3		Ps	Re	167, 168
Phyllostegia hirsuta	39.8	(37–44)	41.1	(35–46)	0.97	(0.9–1.1)	3		Su	Sc	169, 170
Phyllostegia hispida	35	(33–37)	36.3	(35–37)	0.96	(0.9–1.1)	3		Su	Sc	171, 172
Phyllostegia lantanoides	36.3	(35–37)	38.1	(37–40)	0.95	(0.9–1.0)	3		Su	Sc	173
Phyllostegia racemosa	33.2	(33–35)	36.1	(33–37)	0.92	(0.8–1.0)	3		Su	Sc	174
Physostegia longisepala	55.9	(53–59)	48.4	(46–52)	1.16	(1.1–1.3)	3		Su	Sc	175, 176
Physostegia pulchella	45.8	(43–48)	42.3	(36–46)	1.09	(1.0–1.3)	3		Su	Sc	
Prasium majus	35.9	(33–40)	30.6	(26–44)	1.19	(0.9–1.4)	3		Su	Sc	177

TABLE 2. Continued.

Species	Polar axis (μm)		Equatorial axis (μm)		P/E ratio		Colpi	Columellae	Sculpturing		Figures
	Mean	Range	Mean	Range	Mean	Range			Upper	Lower	
Pseuderemostachys sewertzowii	37.0	(31–42)	29.0	(26–31)	1.28	(1.0–1.5)	3		Su	Sc	178, 179
Roylea cinerea	22.2	(20–24)	22.0	(20–24)	1.02	(0.8–1.2)	3		Su	Sc/Mi	180, 181
Sideritis canariensis	31.7	(31–33)	35.0	(33–37)	0.91	(0.8–1.0)	4		Ps	Sc	182, 183
Sideritis candicans	44.0	(42–46)	40.3	(35–44)	1.10	(1.0–1.3)	4		Ps	Sc	184
Sideritis chlorostegia	30.4	(29–33)	30.4	(29–33)	1.00	(—)	6		Ps	Sc	191, 192
Sideritis curvidens	26.6	(24–29)	22.2	(20–24)	1.20	(1.1–1.3)	4		Ps	Sc	185
Sideritis euboea	31.7	(29–33)	31.7	(29–33)	1.00	(—)	6		Ps	Sc	193
Sideritis gomerae	36.3	(35–40)	33.9	(31–37)	1.08	(0.9–1.2)	4		Ps	Sc	
Sideritis hirsuta	31.9	(31–33)	29.7	(26–33)	1.08	(1.0–1.2)	4		Ps	Sc	
Sideritis hololeuca	31.5	(29–33)	31.5	(29–33)	1.00	(—)	6		Ps	Sc	194
Sideritis hyssopifolia	27.5	(24–31)	25.5	(22–29)	1.09	(0.9–1.4)	4		Ps	Sc	186
Sideritis ilicifolia	32.8	(31–35)	24.9	(22–29)	1.33	(1.2–1.5)	4		Ps	Sc/Pu	187
Sideritis incana	26.2	(24–29)	24.6	(24–26)	1.06	(1.0–1.2)	4		Ps	Sc	
Sideritis lagascana	31.2	(29–33)	24.0	(22–26)	1.31	(1.1–1.4)	4	Simple	Ps	Sc	188
Sideritis lanata	29.7	(29–33)	28	(26–31)	1.07	(0.9–1.6)	4		Ps	Sc	
Sideritis libanotica	28.6	(26–31)	28.6	(26–31)	1.00	(—)	6		Ps	Sc	
Sideritis marshchalliana	30.5	(29–33)	30.5	(29–33)	1.00	(—)	6		Ps	Sc	
Sideritis montana	26.4	(24–29)	25.7	(20–29)	1.03	(0.9–1.3)	3		Ps	Sc+Fo	195, 196
Sideritis pullulans	35.2	(31–40)	35.2	(33–37)	1.00	(0.9–1.1)	6		Ps	Sc	
Sideritis romana	26.0	(24–29)	21.3	(20–24)	1.22	(1.1–1.3)	4		Ps	Sc	189
Sideritis villosa	30.7	(29–33)	28.4	(26–31)	1.07	(0.9–1.2)	4		Ps	Sc	190
Stachyopsis oblongata	23.3	(22–24)	21.6	(20–24)	1.09	(0.9–1.2)	3	Simple	Su	Sc	197–199
Stachys riddellii							3		Su	Sc	200, 201
Stachys sylvatica	28.2	(26–31)	24.4	(24–26)	1.15	(1.1–1.3)	3	Simple	Su	Sc	202–204
Stenogyne haliakalae	39.6	(35–44)	36.5	(33–42)	1.09	(1.0–1.2)	3	Branched?	Su	Sc	205, 206
Stenogyne kamehamehae	45.8	(44–48)	41.4	(40–44)	1.11	(1.0–1.2)	3		Su	Sc	207, 208
Stenogyne purpurea	38.5	(33–44)	31.7	(28–35)	1.22	(1.0–1.4)	3	Simple	Su	Sc	209, 210
Sulaimania otostegioides	21.6	(20 22)	20.0	(19–22)	1.08	(0.9–1.1)	3		Su	Sc	211

TABLE 2. Continued.

Species	Polar axis (μm)		Equatorial axis (μm)		P/E ratio		Colpi	Columellae	Sculpturing		Figures
	Mean	Range	Mean	Range	Mean	Range			Upper	Lower	
Suzukia luchuensis	27.1	(24–29)	24.2	(22–26)	1.12	(1.0–1.3)	3		Su	Sc	212, 213
Synandra hispidula	40.3	(39–42)	30.8	(29–33)	1.31	(1.2–1.4)	3	Simple	Su	Sc	214, 215
Thuspeinanta persica	39.6	(33–42)	29.7	(24–35)	1.35	(1.0–1.6)	3		Su	Sc	216, 217
Wiedemannia orientalis	25.1	(24–29)	18.0	(15–20)	1.40	(1.2–1.7)	3		Su	Sc	218, 219
Subfamily Pogostemonoideae											
Colebrookea oppositifolia	18.7	(18–22)	18.9	(15–20)	0.99	(0.9–1.3)	3	Simple	Su	Sc	240, 241
Comanthosphace japonica	23.5	(22–26)	19.4	(18–22)	1.22	(1.0–1.4)	3		Su	Sc	242–244
Comanthosphace stellipila	24.2	(20–26)	20.0	(18–22)	1.23	(0.9–1.5)	3		Su	Sc	
Comanthosphace sublanceolata	22.0	(20–24)	18.5	(15–22)	1.20	(1.0–1.4)	3		Su	Sc	
Leucosceptrum canum	27.1	(24–29)	24.9	(24–26)	1.09	(1.0–1.2)	3	Simple	Su	Sc	245, 246
Pogostemon brachystachyus	26.0	(24–29)	23.1	(22–24)	1.12	(1.1–1.3)	3		Su	Sc	227, 228
Pogostemon cablin	26.0	(—)	24.2	(22–26)	1.09	(1.0–1.2)	3		Su	Sc	229, 230
Pogostemon cruciatus	24.9	(24–26)	26.4	(24–29)	0.95	(0.9–1.0)	3		Su	Mi	231
Pogostemon glaber	24.9	(20–29)	19.4	(18–22)	1.30	(0.9–1.5)	3		Su	Mi	232, 233
Pogostemon heyneanus	27.3	(26–29)	20.2	(18–22)	1.35	(1.2–1.6)	3		Su	Sc	
Pogostemon myosuroides	23.8	(20–24)	17.4	(15–20)	1.37	(1.1–1.6)	3		Su	Mi	234, 235
Pogostemon plectranthoides	27.1	(24–29)	23.5	(20–26)	1.16	(1.1–1.2)	3		Su	Mi	236, 237
Pogostemon sampsonii	**24.0**	(—)	**22.0**	(—)	**1.10**	(—)	**3**		**Su**	**?**	
Pogostemon stellatus	18.7	(15–22)	16.5	(15–18)	1.15	(0.9–1.4)	3		Su	?	
Pogostemon yatabeanus	24.2	(22–26)	18.7	(15–22)	1.31	(1.0–1.7)	3		Su	Mi	238, 239
Rostrinucula dependens	23.1	(22–26)	21.8	(20–22)	1.06	(1.0–1.2)	3		Su	Sc	247
Genera of uncertain affinities											
Anisomeles heyneana	27.0	(24–29)	25.1	(22–29)	1.09	(0.9–1.3)	3		Su	Mi	220
Anisomeles indica	31.2	(29–35)	32.1	(29–35)	0.98	(0.8–1.2)	3		Su	Mi	221, 222
Anisomeles malabarica	35.2	(33–40)	34.1	(31–37)	1.04	(0.9–1.3)	3		Su	Mi	223
Anisomeles salviifolia	28.2	(26–31)	25.5	(24–26)	1.11	(1.0–1.3)	3		Su	Mi	224, 225
Eurysolen gracilis	23.8	(22–26)	18.9	(18–20)	1.26	(1.1–1.5)	3	Simple	Su	Sc	226

rest of the grain scrobiculate); columellae simple (Nabli, 1976).

POGOSTEMONOIDEAE

Pollen of subfamily Pogostemonoideae (Figs. 227–247) is oblate spheroidal to euprolate, with the polar axis 15–29 μm and the equatorial axis 15–29 μm. The grains are tricolpate and inoperculate. The exine is scrobiculate or microreticulate, with suprareticulate sculpturing (poorly developed in *Rostrinucula*, approaching a psilate condition). In some species of *Pogostemon* (Figs. 231, 235; Pozhidaev, 1989), the lumina contain one or more large central perforations surrounded by small ones. The columellae are unbranched.

DISCUSSION

Pollen morphology provides no distinction between subfamilies Lamioideae and Pogostemonoideae, the variation within the former encompassing that found in the latter. At a lower taxonomic level, similar pollen features suggest relationships within and between certain genera. In some cases, these similarities are thought to be derived, based on a previous cladistic analysis of a more inclusive study group (Cantino, 1992a; see below), and can therefore be cited as putative synapomorphies (de Pinna, 1991) until they are tested for congruence with other characters through a parsimony analysis. Other features are not clearly ancestral or derived and therefore contribute only to an assessment of phenetic relationship.

Based on outgroup comparison to the Scrophulariales, we argued (Abu-Asab & Cantino, 1992) that the following pollen character states are plesiomorphic in the Labiatae: three apertures, absence of operculum, simple columellae, psilate exine. We further hypothesized that suprareticulate sculpturing is a synapomorphy of a large clade comprising the gynobasic-styled Labiatae (including all taxa under study here), some of the genera of Labiatae that lack a gynobasic style, and a few genera traditionally assigned to the Verbenaceae. This hypothesis was corroborated by a cladistic analysis of 85 characters (Cantino, 1992a), five of which pertained to pollen. Within the clade marked by suprareticulate pollen, subfamilies Lamioideae and Pogostemonoideae occupy a relatively derived position. Therefore, although suprareticulate sculpturing is apomorphic in the Labiatae as a whole, it is plesiomorphic within the groups of concern here (Cantino, 1992a). Thus, the plesiomorphic pollen type in subfamilies Lamioideae and Pogostemonoideae is tricolpate, inoperculate, with suprareticulate sculpturing and simple columellae. All of the Pogostemonoideae, most Lamioideae, and the two genera of uncertain affinities exhibit these plesiomorphic conditions, but the following derived states occur in some Lamioideae: tetracolpate and 6-pantocolpate pollen, branched columellae, and four forms of sculpturing (psilate, granulate, rugulate, and suprareticulate-rugulate).

NUMBER OF APERTURES

Within the study group, hexapantocolpate pollen (Figs. 191, 194) was found in *Sideritis* sect. *Empedoclea*. Elsewhere in the family, this feature has been reported in only three species (traditionally assigned to the Verbenaceae but treated here as Labiatae, following Cantino et al., 1992): *Caryopteris nepalensis* Moldenke, *Clerodendrum citrinum* Ridley, and *Huxleya linifolia* Ewart & B. Rees (Abu-Asab et al., 1993). These species are only distantly related to subfamily Lamioideae (Cantino, 1992a). Because 6-pantocolpate pollen is a derived condition (Cantino, 1992a), it can be treated as a putative synapomorphy of *Sideritis* sect. *Empedoclea* pending a test for congruence with other characters. Although we examined only five species, Huynh (1972) studied many others and found this feature to be constant within the section and absent elsewhere in the genus.

Tetracolpate grains (a derived state) were observed in *Haplostachys*, *Marrubium anisodon*, and many species of *Sideritis*. In *Haplostachys*, the colpi are arranged in two pairs (Fig. 53), whereas the colpi are equally spaced in *Sideritis* (Figs. 182, 186, 189); the colpal arrangement in *Marrubium anisodon* is unclear (Fig. 122). In *Sideritis*, tetracolpate pollen delimits a clade comprising four of the six sections (Huynh, 1972). In both examined species of *Haplostachys*, tricolpate and tetracolpate grains were found in the same flower, thus their presence may not be a reliable feature of the genus.

COLUMELLAR STRUCTURE

Simple columellae are plesiomorphic and found in most gynobasic-styled Labiatae (Abu-Asab & Cantino, 1992). The only apparent exceptions we are aware of within the Lamioideae or Pogostemonoideae are *Gomphostemma* (Figs. 66, 72), *Bostrychanthera* (Pozhidaev, 1989), *Chelonopsis lichiangensis* (Fig. 32), and perhaps *Stenogyne haliakalae* Wawra (Fig. 206). In the latter, some columellae seem to branch apically while others appear to be simple. It is unclear from the few available photographs whether the branched struc-

tures are columellae or elements of the tectum. Further TEM study of these genera would help clarify the situation.

It is noteworthy that three of the genera in which these branched structures have been observed (viz., *Bostrychanthera*, *Gomphostemma*, and *Stenogyne*) are members of tribe Prasieae sensu Wunderlich (1967) (= subfamily Prasioideae sensu Briquet, 1895–1897), a group of six genera distinguished by fleshy nutlets. The columellar structure should be examined in the other three genera (*Haplostachys*, *Phyllostegia*, and *Prasium*), and further study of *Chelonopsis* would be worthwhile. Branched columellae (if that is indeed what they are) are derived within the Lamioideae and may therefore provide evidence for a relationship between *Chelonopsis* and tribe Prasieae.

DERIVED FORMS OF SCULPTURING

Most of the species studied have supratectal sculpturing of some sort (usually suprareticulate), but the following taxa have psilate pollen: *Lamiophlomis* (Figs. 78, 79), *Marrubium* (Figs. 122–128), *Notochaete* (Figs. 140, 141), *Phlomidoschema* (Figs. 157, 158), *Phyllostegia grandiflora* (Figs. 167, 168), *Sideritis* (Figs. 182–196), and some species of *Gomphostemma* (Figs. 65, 72). Although the term "psilate" is sometimes restricted to tectate pollen, we apply it here to any grain lacking supratectal or supramural sculpturing. Most of the psilate species have a scrobiculate exine (bordering on punctate in some species of *Marrubium* and *Sideritis*), but it is reticulate in *Phyllostegia grandiflora* and microreticulate in *Gomphostemma intermedium*. In *Sideritis montana* (Figs. 195, 196) and *S. remota* (Huynh, 1972), foveolate zones are localized in five distinct areas, two at the poles and three on the mesocolpia; the rest of the surface is scrobiculate.

The evolution of psilate grains in the Lamioideae is a reversal because suprareticulate sculpturing (plesiomorphic in the Lamioideae) evolved from psilate ancestors (Abu-Asab & Cantino, 1992; Cantino, 1992a). One must be cautious about inferring relationships based on this feature because the transformation of suprareticulate to psilate grains has occurred several times in the Labiatae (Wagstaff, 1992). An intermediate condition may be represented in one genus of Lamioideae (*Metastachydium*, Fig. 121) and one of Pogostemonoideae (*Rostrinucula*, Fig. 247). Two of the genera with psilate pollen (*Sideritis* and *Marrubium*) have long been grouped together on the basis of floral morphology (Bentham, 1832–1836, 1876; Briquet, 1895–1897), but the other psilate taxa are not thought to be related to them.

The psilate pollen of *Lamiophlomis* supports (at least on phenetic grounds) its segregation from *Phlomis*, as pointed out by Azizian & Moore (1982), and the psilate pollen of *Phlomidoschema* supports its segregation from *Stachys*. In all such cases in which a genus is segregated on the basis of a putative apomorphy, its segregation is provisional pending phylogenetic study of the larger complex it belongs to. Ideally, it should be demonstrated that both the segregate and the taxon it is segregated from have synapomorphies; otherwise removal of the segregate may create a paraphyletic group.

The distribution of granulate sculpturing may be systematically significant in *Gomphostemma*, *Lamium*, and *Phlomis*. Within the latter, it was found only in *P. maximoviczii* and *P. umbrosa* (Figs. 163, 166). The other species of *Phlomis* that we examined, the five species studied by Ubera & Galán (1983), and the six species of *Phlomis* s. str. (i.e., excluding *P. rotata* Benth. [= *Lamiophlomis*]) illustrated by Azizian & Moore (1982) all have suprareticulate pollen. The species with granulate pollen (also the smallest grains in the genus; Table 2) are both found in northern China and belong to section *Phlomoides* (Moench) Briq. (Briquet, 1895–1897). Other species in this section have suprareticulate pollen (e.g., *P. agraria*, Figs. 159, 160; Azizian & Moore, 1982).

Within *Lamium*, both species with granulate sculpturing (*L. album* and *L. moschatum*) fall within section *Lamiotypus* Dumort. sensu Mennema (1989). More generally, the variation in sculpturing found in Lamium correlates well with Mennema's classification. This is not the case in *Gomphostemma*, where the distribution of sculpturing types is incongruent with the sectional classification used by Briquet (1895–1897) and Wu & Li (1977). The two species with granulate sculpturing (*G. chinense* and *G. parviflorum*) fall into different sections. At least three sculpturing types (Figs. 63, 65, 70) are represented within section *Gomphostemma* and two (Figs. 68, 74) within section *Stenostoma* Prain.

Rugulate sculpturing was found in *Gomphostemma javanicum* (Fig. 70) and *Lagopsis marrubiastrum* (Fig. 77). Although both are described here as rugulate, the sculpturing is quite different in appearance. Moreover, the rugulate sculpturing in *Lagopsis* is confined to the mesocolpium; the surface becomes psilate toward the poles. It would be worth determining whether this unique pollen type occurs in the other three species of *Lagopsis*,

as it may be a synapomorphy for the genus and supporting evidence for its segregation from *Marrubium*. All examined species of *Marrubium* s. str. have psilate pollen (Figs. 122–128).

Suprareticulate-rugulate sculpturing, found in *Paraphlomis javanica* (Fig. 153), is marginally distinct from suprareticulate; it differs in that the undulating muri are discontinuous in places and do not consistently anastomose to form lumina, so the supratectal ornamentation varies from reticulate to rugulate on a single grain; furthermore, the muri are granulate (more apparent in the micrographs of Azizian & Moore (1982)). *Paraphlomis oblongifolia* (Blume) Prain has similar sculpturing but with more densely granulate muri (Azizian & Moore, 1982); the other two species of *Paraphlomis* studied have suprareticulate sculpturing (Figs. 155, 156).

VARIANTS OF SUPRARETICULATE SCULPTURING

Within the general class of surpareticulate sculpturing, there is variation in the shape and height of the muri, the size and shape of the lumina, and the number, size, shape, and arrangement of the perforations. It is difficult to assess the polarity of these characters due to variation in the outgroups, but similarities in the sculpturing of certain taxa deserve comment.

The similar sculpturing of *Lamium galeobdolon* (Fig. 87) and *L. flexuosum* (Fig. 82) supports Mennema's (1989) circumscription of *Lamium* subg. *Galeobdolon* (Adans.) Asch. *Lamium galeobdolon* is frequently segregated as the genus *Galeobdolon* Adans. or *Lamiastrum* Heist. ex Fabr., but pollen morphology supports its inclusion within *Lamium*.

The Japanese endemic *Ajugoides humilis* has been variably assigned to *Ajuga*, *Lamium*, *Loxocalyx*, *Stachys*, and the monotypic *Ajugoides* (Kudo, 1929). Its suprareticulate exine sculpturing, with large and sometimes incomplete lumina (Fig. 13), does not resemble that of *Ajuga* (Abu-Asab & Cantino, 1993a), *Lamium* (Figs. 80–91), *Loxocalyx* (Figs. 101–103), or most species of *Stachys* (Figs. 200–204; Bassett & Munro, 1986; Demissew & Harley, 1992). Similar sculpturing occurs in one Mexican species of *Stachys* (*S. tenerrima* Epling; figs. 19, 20 of Bassett & Munro, 1986) and some species of *Scutellaria* (Abu-Asab, 1990). *Ajugoides* is unlikely to be closely related to *Scutellaria*, from which it differs greatly in flower and fruit morphology. It is best retained for now as a monotypic genus, but a relationship to *Stachys* should be investigated.

The only endemic North American genera in subfamily Lamioideae are four members of subtribe Melittidinae sensu Bentham (1848): *Brazoria*, *Macbridea*, *Physostegia*, and *Synandra*. Similarity in stomatal configurations (Cantino, 1990) suggests that *Brazoria*, *Physostegia*, and *Macbridea* form a clade. However there is only weak support for a relationship between these three genera and *Synandra* (Abu-Asab & Cantino, 1987), and no evidence that the remaining genera of Melittidinae, *Melittis* (European) and *Chelonopsis* (Eastern Asian), are related to the four North American genera. A similar picture emerges from the pollen data. Neither *Chelonopsis* (Figs. 31–34) nor *Melittis* (Figs. 119, 120) resembles any of the North American Melittidinae in pollen morphology. The exine sculpturing is quite similar in *Brazoria* (Figs. 23–27), *Macbridea* (Figs. 104–106), and *Physostegia* (Figs. 175, 176; for higher magnification, see Cantino, 1982; Trudel & Morton, 1992). All three have unusually minute perforations and angular muri; in *Physostegia* and some species of *Brazoria*, the shallow lumina are bounded by gradually sloping muri.

Synandra (Fig. 214) differs in sculpturing from *Macbridea*, *Brazoria*, and *Physostegia* but resembles *Galeopsis* (Figs. 46–50). Although a close relationship between *Synandra* and *Galeopsis* has not previously been suggested, they share a distinctive form of suprareticulate sculpturing, with elongate perforations that tend to radiate out from the center of well-defined lumina. Moreover, *Synandra* and *Galeopsis* share two putative synapomorphies. Both are monocarpic (*Galeopsis* is annual and *Synandra* biennial), a derived condition in the Labiatae (Cantino, 1992a). Both have distinct anther thecae; confluent thecae are plesiomorphic in the Lamioideae (Cantino, 1992a).

GENERA OF UNCERTAIN AFFINITIES

Two genera of uncertain subfamilial affinities, *Anisomeles* and *Eurysolen*, were included in the study with the hope that pollen morphology might clarify their position. The monotypic genus *Eurysolen* has been assigned to widely divergent positions in the Labiatae. It was described by Prain (1898), who placed it in the Prasieae (Lamioideae) near *Gomphostemma*. Mukerjee (1940) and Wu & Li (1977) placed *Eurysolen* in the Ajugoideae. Keng (1969) noted a close resemblance to *Achyrospermum* (Lamioideae) in general habit, inflorescence, and floral structure. Press (1982) included the genus within the Pogostemonoideae and pointed out similarities with *Pogostemon*, *Rostrinucula*, and *Comanthosphace*. Unfortunately, pol-

len morphology is of little help in resolving the affinities of *Eurysolen*. Its sculpturing (Fig. 226) resembles species of *Achyrospermum* (Fig. 4), *Comanthosphace* (Fig. 244), and *Ajuga* (Abu-Asab & Cantino, 1993a).

Anisomeles was assigned by Bentham (1848, 1876) and Briquet (1895–1897) to tribe Lamieae (corrected nomenclature follows Sanders & Cantino, 1984), but it lacks characteristic embryological and chemical traits of subfamily Lamioideae (Wunderlich, 1967; Abu-Asab & Cantino, 1987; Cantino, 1992a). Cantino (1992a, b) hypothesized a close relationship between *Anisomeles* and *Pogostemon* based on three synapomorphies: presence of subsessile leaf epidermal glands with a unicellular cap, bearded stamen filaments, and a lustrous pericarp. On the basis of this evidence, Cantino et al. (1992) provisionally assigned *Anisomeles* to subfamily Pogostemonoideae. The distinctive suprareticulate sculpturing of *Anisomeles*, with its regular, polygonal lumina and relatively large perforations (Figs. 220–225), is very similar to that of Pogostemon (Figs. 227–239), supporting the hypothesized relationship between these genera. Within the Lamioideae, similar sculpturing was found in some species of *Microtoena* (Figs. 129–136).

Literature Cited

Abu-Asab, M. S. 1990. Phylogenetic Implications of Pollen Morphology in Subfamily Lamioideae (Labiatae) and Related Taxa. Ph.D. Dissertation. Ohio University, Athens.

——— & P. D. Cantino. 1987. Phylogenetic implications of leaf anatomy in subtribe Melittidinae (Labiatae) and related taxa. J. Arnold Arbor. 68: 1–34.

——— & ———. 1989. Pollen morphology of *Trichostema* (Labiatae) and its systematic implications. Syst. Bot. 14: 359–369.

——— & ———. 1992. Pollen morphology in subfamily Lamioideae (Labiatae) and its phylogenetic implications. Pp. 97–112 *in* R. M. Harley & T. Reynolds (editors), Advances in Labiate Science. Royal Botanic Gardens, Kew.

——— & ———. 1993a. Phylogenetic implications of pollen morphology in tribe Ajugeae (Labiatae). Syst. Bot. 18: 100–122.

——— & ———. 1993b. Systematic implications of pollen morphology in tribe Prostantheraeae (Labiatae). Syst. Bot. 18: 563–574.

———, P. D. Cantino, J. W. Nowicke & T. Sang. 1993. Systematic implications of pollen morphology in *Caryopteris* (Labiatae). Syst. Bot. 18: 502–515.

Airy Shaw, H. K. 1973. A Dictionary of the Flowering Plants and Ferns, 8th ed. (originally by J. C. Willis, revised by Airy Shaw). Cambridge Univ. Press, Cambridge, England.

Azizian, D. & D. M. Moore. 1982. Morphological and palynological studies in *Phlomis* L., *Eremostachys* Bunge and *Paraphlomis* Prain (Labiatae). Bot. J. Linn. Soc. 85: 225–248.

Bassett, I. J. & D. B. Munro. 1986. Pollen morphology of the genus *Stachys* (Labiatae) in North America, with comparisons to some taxa from Mexico, Central and South America and Eurasia. Pollen & Spores 28: 279–296.

Bentham, G. 1832–1836. Labiatarum Genera et Species. Ridgway & Sons, London.

———. 1848. Labiatae. Pp. 27–603 *in* A. de Candolle (editor), Prodromus Systematis Naturalis Regni Vegetabilis, vol. 12. Treuttel & Würtz, Paris.

———. 1876. Labiatae. Pp. 1160–1223 *in* G. Bentham & J. D. Hooker (editors), Genera Plantarum, vol. 2. Reeve, London.

Briquet, J. 1895–1897. Labiatae. Pp. 183–375 *in* A. Engler & K. Prantl (editors), Die Natürlichen Pflanzenfamilien, Teil 4, Abt. 3a. W. Englemann, Leipzig.

Cantino, P. D. 1982. A monograph of the genus *Physostegia* (Labiatae). Contr. Gray Herb. 211: 1–105.

———. 1990. The phylogenetic significance of stomata and trichomes in the Labiatae and Verbenaceae. J. Arnold Arbor. 71: 323–370.

———. 1992a. Evidence for a polyphyletic origin of the Labiatae. Ann. Missouri Bot. Gard. 79: 361–379.

———. 1992b. Toward a phylogenetic classification of the Labiatae. Pp. 27–37 *in* R. M. Harley & T. Reynolds (editors), Advances in Labiate Science. Royal Botanic Gardens, Kew.

———, R. M. Harley & S. J. Wagstaff. 1992. Genera of Labiatae: Status and classification. Pp. 511–522 *in* R. M. Harley & T. Reynolds (editors), Advances in Labiate Science. Royal Botanic Gardens, Kew.

——— & R. W. Sanders. 1986. Subfamilial classification of Labiatae. Syst. Bot. 11: 163–185.

Demissew, S. & M. M. Harley. 1992. Trichome, seed surface and pollen characters in *Stachys* (Lamioideae: Labiatae) in tropical Africa. Pp. 149–166 *in* R. M. Harley & T. Reynolds (editors), Advances in Labiate Science. Royal Botanic Gardens, Kew.

Downie, S. R. & J. D. Palmer. 1992. Restriction site mapping of the chloroplast DNA inverted repeat: A molecular phylogeny of the Asteridae. Ann. Missouri Bot. Gard. 79: 266–283.

Erdtman, G. 1945. Pollen morphology and plant taxonomy. IV. Labiatae, Verbenaceae, and Avicenniaceae. Svensk Bot. Tidskr. 39: 279–285.

———. 1960. The acetolysis method. A revised description. Svensk Bot. Tidskr. 54: 561–564.

Harley, M. M., A. Paton, R. M. Harley & P. G. Cade. 1992. Pollen morphological studies in tribe Ocimeae (Nepetoideae: Labiatae): I. *Ocimum* L. Grana 31: 161–176.

Holmgren, P. K., N. H. Holmgren & L. C. Barnett. 1990. Index Herbariorum, Part I: The Herbaria of the World, 8th ed. New York Botanical Garden, New York.

Huang, T. C. 1972. Pollen Flora of Taiwan. National Taiwan Univ. Botany Department Press, Taipei.

Huynh, K. L. 1972. Le pollen et la systématique du genre *Sideritis* L. (Labiatae). Bull. Mus. Hist. Nat. (Paris), 3rd series, no. 45, Bot. 1: 1–26.

Keng, H. 1969. Flora Malesianae precursores XLVIII.

A revision of Malesian Labiatae. Gard. Bull. Straits Settlem. 24: 13–180.

KUDO, Y. 1929. Labiatarum sino-japonicarum prodromus. Mem. Fac. Sci. Agr. Taihoku Imperial Univ. 2(2): 1–303.

MABBERLEY, D. J. 1987. The Plant-book. Cambridge Univ. Press, Cambridge, England.

MENNEMA, J. 1989. A Taxonomic Revision of *Lamium* (Lamiaceae). Leiden Bot. Ser., vol. 11. E. J. Brill, Leiden.

MUKERJEE, S. K. 1940. A revision of the Labiatae of the Indian Empire. Rec. Bot. Surv. India 14(1): 1–228.

NABLI, M. A. 1976. Étude ultrastructurale comparée de l'exine chez quelques genres de Labiatae. Pp. 499–525 *in* I. K. Ferguson & J. Muller (editors), The Evolutionary Significance of the Exine. Academic Press, London.

PINNA, M. C. C. DE. 1991. Concepts and tests of homology in the cladistic paradigm. Cladistics 7: 367–394.

POZHIDAEV, A. E. 1989. Exine structure in pollen grains of the Lamiaceae family. Bot. Zurn. 74: 1410–1422.

———. 1992. The origin of three- and six-colpate pollen grains in the Lamiaceae. Grana 31: 49–52.

PRAIN, D. 1898. On three new genera of plants from the Kachin Hills. Sci. Mem. Medical Officers Army India 11: 41–44.

PRESS, J. R. 1982. Taxonomic studies in the Labiatae tribe Pogostemoneae. Bull. Brit. Mus. (Nat. Hist.), Bot. 10: 1–89.

RISCH, C. 1956. Die Pollenkörner der Labiaten. Willdenowia 1: 617–641.

ROCA SALINAS, A. 1978. Estudios morfológicos iniciales del polen de Labiatae L. en la Macaronesia. Bot. Macaronésica 6: 9–25.

SANDERS, R. W. & P. D. CANTINO. 1984. Nomenclature of the subdivisions of the Lamiaceae. Taxon 33: 64–72.

TRUDEL, M. D. G. & J. K. MORTON. 1992. Pollen morphology and taxonomy in North American Labiatae. Canad. J. Bot. 70: 975–995.

UBERA, J. L. & C. GALAN. 1983. Contribución al conocimiento palinológico del género *Phlomis* L. (Labiatae) en la Península Ibérica. Pp. 185 197 *in* N. Solé de Porta & M. Suárez Cervera (editors), Actas del IV Simposio de Palinología (APLE, Barcelona, 1982). Univ. de Barcelona, Spain.

VARGHESE, T. M. & D. P. S. VERMA. 1968. Pollen morphology of some Indian Labiatae. J. Palynol. 4: 77–83.

VEZEY, E. L., V. P. SHAH & J. J. SKVARLA. 1992. A numerical approach to pollen sculpture terminology. Pl. Syst. Evol. 181: 245–254.

WAGSTAFF, S. J. 1992. A phylogenetic interpretation of pollen morphology in tribe Mentheae (Labiatae). Pp. 113 124 *in* R. M. Harley & T. Reynolds (editors), Advances in Labiate Science. Royal Botanic Gardens, Kew.

WALKER, J. W. & J. A. DOYLE. 1975. The bases of angiosperm phylogeny: Palynology. Ann. Missouri Bot. Gard. 62: 644–723.

WATERMAN, A. H. 1960. Pollen grain studies of the Labiatae of Michigan. Webbia 15: 399-415.

WU, C. Y. & H. W. LI. 1977. Flora Reipublicae Popularis Sinicae, vol. 65(2). Science Press, Beijing.

WUNDERLICH, R. 1967. Ein Vorschlag zu einer natürlichen Gliederung der Labiaten auf Grund der Pollenkörner, der Samenentwicklung und des reifen Samens. Österr. Bot. Z. 114: 383–483.

APPENDIX. Abbreviated collection data for voucher specimens. Herbarium abbreviations follow Holmgren et al. (1990).

Achyrosperumum aethiopicum Welw.—Malawi, Pumphi District, *Pawek 6606* (MO).

Achyrospermum carvalhi Gürke—Malawi, *LaCroix 3058* (MO).

Achyrospermum cryptanthum Baker—Tanzania, *Frame 44* (MO).

Achyrospermum densiflorum Blume—Thailand, Southwest Province, Kanchanaburi District, *van Beusekom et al. 3739* (K).

Achyrospermum parviflorum S. Moore—Uganda, *Loveridge 217* (MO).

Achyrospermum schimperi (Hochst. ex Briq.) Perkins—Ethiopia, Shoa Province, *Ash 1726* (MO).

Acrotome angustifolia G. Taylor—Zambia, Barotseland, *Robinson 6789* (MO).

Acrotome hispida Benth.—South Africa, Transvaal, *Werdermann & Oberdieck 1281* (A).

Acrotome inflata Benth.—Botswana, *Galloway 505* (MO).

Acrotome fleckii (Gürke) Launert—Namibia, *Seydel 2675* (A).

Ajugoides humilis (Miq.) Makino—Japan, Yama-jio, *Anonymous* (US 350854); Nagasaki, *Maximowicz s.n.* (BM).

Alajja rhomboidea (Benth.) Ikonn.-Gal.—Afghanistan, Kurrum Valley, *Aitchison 831* (GH).

Anisomeles heyneana Benth.—India, Mumbra, 2 Dec. 1950, *Santapau s.n.* (MO).

Anisomeles indica (L.) Kuntze—India, Hassan District, *Saldanha & Gandhi 2170* (MO). China, Hainan, *Chun & Tso 43882* (MO).

Anisomeles malabarica (L.) R. Br. ex Sims—India, Hassan District, *Saldanha 16079* (MO).

Anisomeles salviifolia R. Br.—Australia, Northern Territory, *Adams 1755* (K).

Ballota africana Benth.—South Africa, *Perry & Snijman 2313* (MO).

Ballota andreuzziana Pamp.—Libya, Kouf National Park, "*J.H.H. L67*" (K).

Ballota hirsuta Benth.—Morocco, N of Tafraoute, "*B M. Exped. 422*" (MO).

Ballota integrifolia Benth.—Cyprus, Paphos District. *Davis 3405* (K).

Ballota nigra L.—U.S.A., Ohio, Athens County, *Cantino 1300* (BHO). Italy, Cicilia, *Larsen, Larsen & Nielsen 35996* (MO).

Ballota pseudodictamnus (L.) Benth.—U.S.A., Ohio, Athens (cultivated), *Cantino 1329* (BHO).

Ballota rupestris (Biv.) Vis.—U.S.A, Ohio, Athens (cultivated), *Cantino 1310* (BHO).

Brazoria arenaria Lundell—U.S.A, Texas, Aransas County, *Kessler 5773* (BHO).

Brazoria pulcherrima Lundell—U.S.A, Texas, Leon County, *Kessler 5865* (BHO).

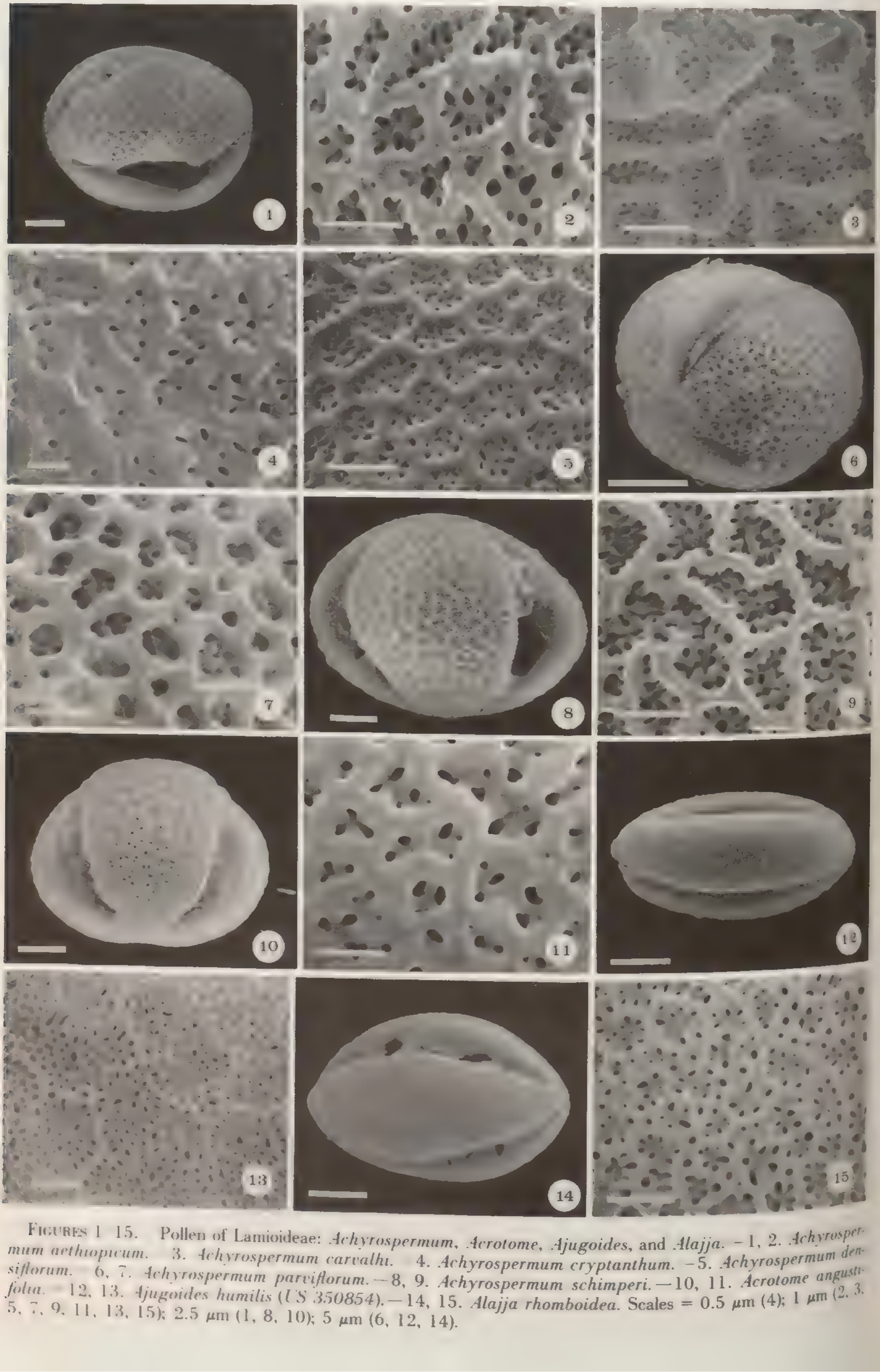
Brazoria scutellarioides Engelm. & A. Gray—U.S.A. Texas, Barton Creek, 15 May 1936, *Tharp s.n.* (GH); Travis County, *Sanders 76179* (TEX).

Brazoria truncata (Benth.) Engelm. & A. Gray—U.S.A.,

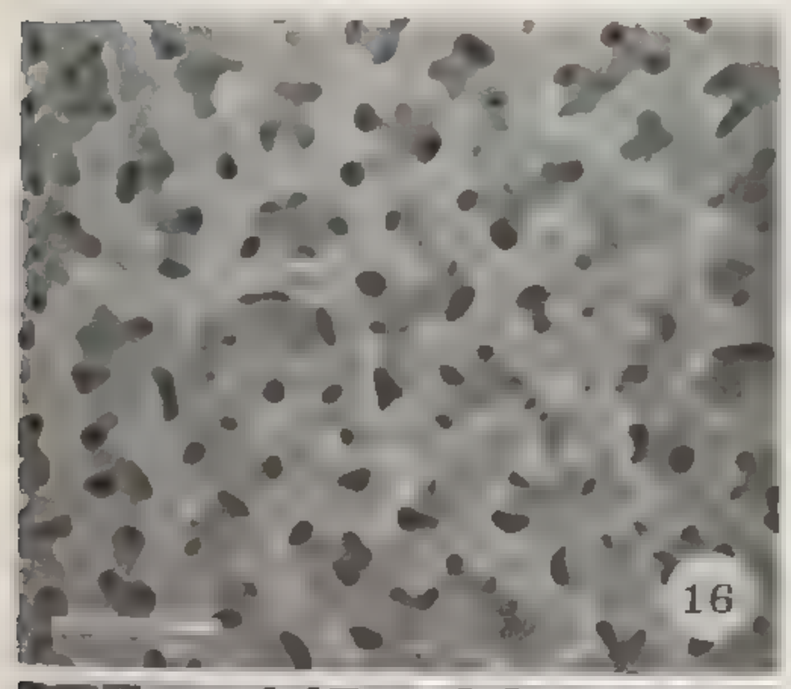
Texas, Live Oak County, *Sanders 76122* (TEX); Burnet County, *Correll & Ogden 25300* (GH).
Chamaesphacos ilicifolius Schrenk—Iran, E Khorasan, *Rechinger 51448* (MO).
Chaiturus marrubiastrum (L.) Spenner—U.S.A., Kansas, Douglas County, *McGregor 12* (US).
Chelonopsis lichiangensis W. Smith—China, Yunnan, *Forrest 15429* (K).
Chelonopsis odontochila Diels—China, Yunnan, Chungtien, *Yu 14923* (A).
Colebrookea oppositifolia Smith—China, Yunnan, *Rock 2348* (A).
Colquhounia coccinea Wallich—China, Yunnan, *Rock 6231* (A).
Colquhounia seguinii Vaniot—China, Yunnan, *Ten 26* (A).
Comanthosphace japonica (Miq.) S. Moore—Japan, Tochigi Pref., 10 Sep. 1975, *Ohashi & Murata s.n.* (A). Japan, 1862, *Anonymous* (US).
Comanthosphace stellipila (Miq.) S. Moore—Japan, Suruga Province, Shidzuoka Pref., 30 Aug. 1958, *Furuse s.n.* (A). Japan, *Makino s.n.* (US).
Comanthosphace sublanceolata (Miq.) S. Moore—Japan, Hondo, *Shiota 7301* (GH).
Craniotome furcata (Link) Kuntze—Nepal, *Banerjo 2864* (US). Nepal, Riala, *Polunin, Sykes & Williams 1297* (A). India, NW Himalayas, *Gupta s.n.* (US).
Eremostachys fetissovii Regel—Kazakhstan, *Goloskokov 4487* (A).
Eremostachys iliensis Regel—Kazakhstan, *Goloskokov 4143* (A).
Eremostachys rotata Schrenk ex Fischer & C. Meyer—Kazakhstan, *Roldugin 4432* (A).
Eremostachys speciosa Rupr.—Kirghizia, *Armand 961* (A).
Eriophyton wallichianum Benth.—China, Tibet, *Ludlow & Sherriff 8859* (GH).
Eurysolen gracilis Prain—Indonesia, Java, *van Steenis 11118* (GH).
Galeopsis bifida Boenn.—Denmark, Zealand, *Svendsen 450* (MO).
Galeopsis ladanum L.—Switzerland, 23 July 1953, *Lohammar s.n.* (MO).
Galeopsis pubescens Besser—Switzerland, Evolene, *Anonymous 3139* (MO).
Galeopsis segetum Necker—U.S.A., Ohio, Athens (cultivated), *Cantino 1339* (BHO).
Galeopsis speciosa Miller—Finland, Nylandia, *Vanhecke 5480* (MO).
Galeopsis tetrahit L.—Canada, Ontario, Algoma District, *Sample & Brammall 2864* (MO).
Gomphostemma chinense Oliver—Thailand, Banang Sta., *Kerr 7346* (K).
Gomphostemma intermedium Craib—Thailand, *Kerr 6347* (K).
Gomphostemma javanicum (Benth.) Benth.—Malaysia, Pahang, *Shah 2772* (A).
Gomphostemma leptodon Dunn—Indochina, Dec. 1926, *Anonymous 5002* (A).
Gomphostemma lucidum Wallich ex Benth.—Thailand, Dai Angka, *Garrett 409* (K).
Gomphostemma parviflorum Wallich ex Benth.—Bangladesh, Chittagong, *Parkinson 4263* (A).
Gomphostemma wallichii Prain—Burma, *J. F. Smith 107* (GH).
Haplostachys haplostachya (A. Gray) H. St. John—U.S.A., Hawaii, Waimea, *Rock 8350* (A).
Haplostachys linearifolia (Drake) Sherff—U.S.A., Hawaii, Mauna Loa, Molokai, Feb. 1910, *Rock s.n.* (GH).
Hypogomphia turkestana Bunge—Afghanistan, Salang Pass, *Hewer 1025A* (K). USSR, Turgaiskaia, *Kraschenninikov 5127* (A).
Lagochilus aucheri Boiss.—Iran, Kurdistan, *Rechinger 42853* (K).
Lagochilus diacanthophyllus (Pallas) Benth.—Kazakhstan, *Goloskokov 5788* (MO).
Lagochilus hirtus Fischer & C. Meyer—Kazakhstan, *Goloskokov 4292* (MO).
Lagopsis marrubiastrum (Stephan) Ikonn.-Gal.—India, *Koelz 6565* (US).
Lagopsis supina (Stephan) Ikonn.-Gal.—China, Hebei, *Beach 17* (K).
Lamiophlomis rotata (Benth.) Kudo—China, Tibet, *Rock 14406* (GH).
Lamium album L.—Iceland, Knappstadhir, *Elseley 55/71* (MO).
Lamium flexuosum Ten.—Italy, Sicilia, *Larsen 35657* (MO).
Lamium galeobdolon (L.) L.—Britain, S Wales, 11 May 1964, *Price s.n.* (MO).
Lamium garganicum L.—Turkey, Malatya, *Balls B2287* (K).
Lamium moluccellifolium Fries—Denmark, Ega District, 26 June 1966, *Benjamin s.n.* (MO).
Lamium moschatum Miller—Cyprus, Liveras, *Meikle 2410* (K).
Lamium purpureum L.—U.S.A, Ohio, Athens County, *Cantino 1273* (BHO).
Leonotis bequaertii De Wild.—Zaire, Katanga Province, Momba Territory, *Dubois 1072* (K).
Leonotis leonitis R. Br.—Kenya, Machakos District, *Verdcourt 2362* (K).
Leonotis mollissima Gürke—Tanzania, Monduli District, *Greenway & Kanuri 12560* (K).
Leonurus cardiaca L.—U.S.A, Minnesota, Houston County, *Swanson 811* (MO). Mexico, Chiapas, *Lellez & Pankhurst 6966* (MO).
Leonurus sibiricus L.—Honduras, *Nichols 2140* (MO).
Leucas abyssinica (Benth.) Briq.—Somalia, Luuq District, *Wieland 1142* (MO).
Leucas alluaudii Sacleux—Burundi, Muramwya, Teza, *Reekmans 10728* (MO).
Leucas aspera (Willd.) Link—China, Hainan, Janfengling, *Chow 78309* (MO).
Leucas biflora R. Br.—Sri Lanka, Yala Bungalow, *Cooray 69010407R* (MO).
Leucas calostachys Oliver—Burundi, Muyinga Province, *Reekmans 6977* (MO).
Leucas ciliata Benth.—India, Hassan District, *Ramamoorthy & Gandhi HFP2602* (MO).
Leucas eriostoma Hook. f.—India, Karnataka Chikmagalur, *Saldanha KFP9600* (MO).
Leucas hirta Sprengel—India, Hassan District, *Saldanha 17909* (MO).
Leucas inflata Benth.—Yemen, Bait al Lakida, *Miller 12* (K).
Leucas javanica Benth.—Indonesia, Celebes, *Meijer 10953* (MO).
Leucas lanata Benth.—India, Mussoorie, *Dudgeon & Kenoyer 37* (MO).
Leucas lavandulifolia Smith—India, Hassan District, *Ramamoorthy HFP1744* (MO).
Leucas marrubioides Desf.—India, *Bembower 169* (MO).

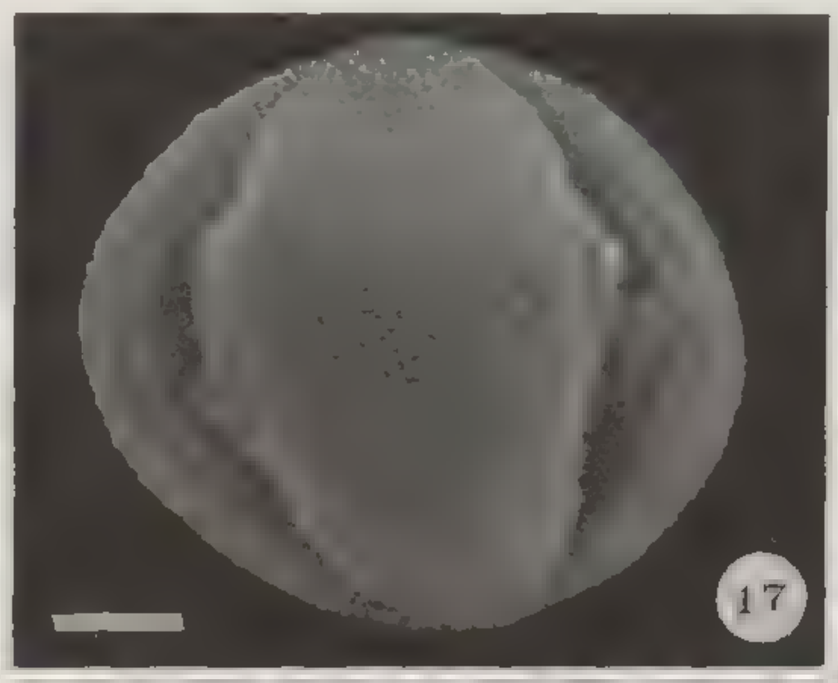
Leucas martinicensis R. Br.—India, Hassan District, Mysore, *Saldanha 15337* (MO).
Leucas mollissima Wallich ex Benth.—Japan, Kagoshima Prefecture, Pyukyu, *Iwatsuki et al. 104* (MO).
Leucas rosmarinifolia Benth.—India, Kodaikanal, *Bembower 331* (MO).
Leucas stelligera Wallich—India, Castle Rock, *Almeida 257* (MO).
Leucosceptrum canum Smith—China, Yunnan, *Rock 6650* (A). Burma, *McMillen 196* (US).
Loxocalyx ambiguus (Makino) Makino—Japan, Yamato Province, *Murata 10748* (A).
Loxocalyx urticifolius Hemsley—China, Hubei, *Henry 6482* (GH).
Macbridea alba Chapman—U.S.A, Florida, Bay County, *Godfrey 79884* (BHO); Apalachicola, *Biltmore Herb. 4199a* (GH).
Macbridea caroliniana (Walter) Blake—U.S.A, North Carolina, Brunswick County, *Radford 6334* (GH).
Marrubium anisodon C. Koch—Afghanistan, Ghorband, *Seybold 36896* (MO).
Marrubium cuneatum Russell—Iraq, Kursi, *Gillett 10852* (K).
Marrubium heterodon (Benth.) Boiss. & Balansa—Turkey, Adana Province, *Davis 16545* (K).
Marrubium incanum Desr.—U.S.A., Ohio, Athens (cultivated), *Cantino 1334* (BHO).
Marrubium supinum L.—Spain, Sierra de Cazorla, *Townsend T46* (K).
Melittis melissophyllum L.—Greece, *Mennega 174* (MO).
Metastachydium sagittatum (Regel) C.Y. Wu & Li—Kirghizia, Tien Shan Mountains, *Medvedeva et al. 251* (A).
Microtoena delavayi Prain—China, Yunnan, *Forrest 15177* (K).
Microtoena insuavis (Hance) Prain ex Briq.—China, Yunnan, *Wang 80582* (A).
Microtoena robusta Hemsley—China, Hubei, *Henry 6482A* (GH).
Microtoena urticifolia Hemsley—China, Yunnan, *McLaren's Collectors P112* (A).
Moluccella laevis L.—U.S.A., Ohio, Athens (cultivated), *Cantino 1328* (BHO).
Moluccella spinosa L.—U.S.A., Ohio, Athens (cultivated), *Cantino 1316* (BHO).
Notochaete hamosa Benth.—India, Assam, *Bor 16154* (A).
Otostegia fruticosa Briq.—Saudi Arabia, *Humbles 10008* (MO).
Otostegia integrifolia Benth.—Ethiopia, *Amshoff 10381* (MO).
Otostegia minuccii Pic.-Serm.—Ethiopia, Addis Ababa, *Meyer 7472* (MO).
Otostegia repanda Benth.—Ethiopia, Sidamo Province, *Ash 1885* (MO).
Otostegia tomentosa A. Rich.—Ethiopia, Debra Zebit, *Boulos 9790* (MO).
Panzerina lanata (L.) Soják—Mongolia, Altai, *Steinberg & Prochorova 3459* (A). Russia, Krasnojarsk Province, *Reverdatto 3775b* (A) [labeled as *Panzeria argyracea*].
Paralamium gracile Dunn—China, Yunnan, *Henry 10636* (K).
Paraphlomis javanica (Blume) Prain ex Backer & Bakh. f.—Indonesia, Sumatra, *Rahmat Si Boeea 9772a* (GH).
Paraphlomis lanceolata Hand.-Mazz.—China, Hunan, Changning Hsien, *Fan & Li 91* (GH).
Paraphlomis rugosa Prain—China, Gwangdong, *Merrill 10741* (A).
Phlomidoschema parviflorum (Benth.) Vved.—Pakistan, Baluchistan, Kurram District, *Siddiqi & Iqbal 94* (A).
Phlomis agraria Bunge—Kazakhstan, *Schipczinsky 802* (A).
Phlomis crinita Cav.—Algeria, Oran Department, *Samuelsson 7071* (GH).
Phlomis herba-venti L.—France, Aude Department, 12 July 1891, *Neyraut s.n.* (GH).
Phlomis lanata Willd.—U.S.A., Ohio, Athens (cultivated), *Cantino 1365* (BHO).
Phlomis maximoviczii Regel—China, Manchuria, *Litvinov 1559* (A).
Phlomis tuberosa L.—U.S.A, Ohio, Athens (cultivated), *Cantino 1294* (BHO).
Phlomis umbrosa Turcz.—China, Shandong Province, *Chiao 2735* (GH).
Phyllostegia grandiflora (Gaudich.) Benth.—U.S.A, Hawaii, Oahu, Palolo Valley, 30 Nov. 1912, *Rock & Ballon s.n.* (GH).
Phyllostegia hirsuta Benth.—U.S.A, Hawaii, Oahu, Mt. Olympus, Apr. 1918, *Rock & Lyon s.n.* (A).
Phyllostegia hispida Hillebr.—U.S.A, Hawaii, Molokai, *Rock 10327* (A).
Phyllostegia lantanoides Sherff—U.S.A, Hawaii, Oahu, *Degener 10038* (GH).
Phyllostegia racemosa Benth.—U.S.A, Hawaii, Molokai, *Rock 6198* (A).
Physostegia longisepala Cantino—U.S.A., Louisiana, Calcasieu Parish, *Gilmore & Smith 3501* (BHO).
Physostegia pulchella Lundell—U.S.A., Texas, Brazoria County, *Brown 9892* (BHO).
Pogostemon brachystachyus Benth.—India, Assam, Khasi Hills, *Hooker & Thomson s.n.* (GH).
Pogostemon cablin (Blanco) Benth.—Puerto Rico, Mayaguez, *Horn 5424* (GH).
Pogostemon cruciatus (Benth.) Kuntze—Nepal, *Strachey & Winterbottom s.n.* (GH).
Pogostemon glaber Benth.—China, Hainan, *McClure s.n.* (Canton Christian College Herb. 8454) (A).
Pogostemon heyneanus Benth.—U.S.A, Ohio, Athens (cultivated), *Cantino 1314* (BHO).
Pogostemon myosuroides (Benth.) Kuntze—India, Malabar Concan, *Stocks, Law & Co. s.n.* (GH).
Pogostemon plectranthoides Desf.—U.S.A, Ohio, Athens (cultivated), *Cantino 1317* (BHO).
Pogostemon sampsonii (Hance) Press—China, Guangdong, Wung Yuen District, *Lau 2549* (GH).
Pogostemon stellatus (Lour.) Kuntze—China, Kwangsi, Kweilin, *Wan & Chow 79176* (A).
Pogostemon yatabeanus (Makino) Press—Japan, Mino Province, Hondo, *Shiota 4267* (GH).
Prasium majus L.—U.S.A., Ohio, Athens (cultivated), *Cantino 1356* (BHO).
Pseuderemostachys sewertzowii (Herder) Popov—Kazakhstan, 12 May 1962, *Karmyscheva s.n.* (MO 1879982).
Rostrinucula dependens (Rehder) Kudo—China, W China, *Wilson 4313* (A).
Roylea cinerea (D. Don) Baillon—India, Chamba District, 27 Apr. 1920, *Parker s.n.* (A).
Sideritis canariensis L.—Spain, Canary Islands, Palma, *Bourgeau 125* (A).
Sideritis candicans Aiton—Spain, Canary Islands, Teneriffe, *Burchard 134* (A).

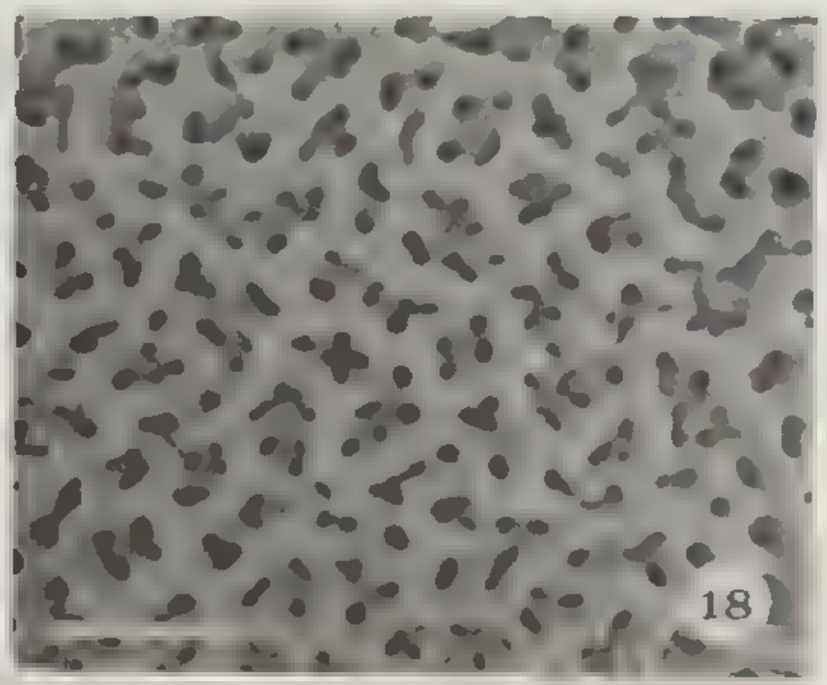
Sideritis chlorostegia Juz.—Ukraine, Crimea, *Juzepczuk 3937* (A).
Sideritis curvidens Stapf—Greece, *Samuelsson & Zander 299* (GH).
Sideritis euboea Heldr.—locality unknown, July 1927, *Purpus s.n.* (A).
Sideritis gomerae Noë ex Bolle—Spain, Canary Islands, 25 May 1894, *Murray s.n.* (K)
Sideritis hirsuta L.—Spain, Aragon, Prov. de Huesca, 20 July 1892, *St. Lager s.n.* (GH).
Sideritis hololeuca Boiss. & Heldr.—Turkey, Konya Province, *Davis 16238* (K).
Sideritis hyssopifolia L.—Spain, Huesca Province, *Brenan 12236* (K).
Sideritis ilicifolia Willd.—Spain, Aragon, Barbastro, 13 July 1892, *St. Lager s.n.* (GH).
Sideritis incana L.—Algeria, 16 July 1894, *Cosson s.n.* (GH).
Sideritis lagascana Willk.—Spain, Granada Province, *Reverchon 1099* (A).
Sideritis lanata L.—Turkey, Bithynia, Bile ik, *Bornmüller 14569* (GH).
Sideritis libanotica Labill.—Syria, *Shepard s.n.* (GH).
Sideritis marschalliana Juz.—Ukraine, Crimea, *Juzepczuk & Vysokoostrovskaja 3939* (A).
Sideritis montana L.—Algeria, Bedeau, 18 June 1934, *Faure s.n.* (GH).
Sideritis pullulans Vent.—Lebanon, *Samuelsson 6150* (MO).
Sideritis romana L.—France, 22 Apr. 1905, *Raine s.n.* (GH).
Sideritis villosa Cosson—Morocco, *Balls B2463* (K).
Stachyopsis oblongata (Schrenk) Popov & Vved.—Afghanistan, Badakshan, *Hedge & Carter 445* (K).
Stachys riddellii House—U.S.A., Ohio, Vinton County, *Cantino 1229* (BHO); Meigs County, Forked Run State Park, *Wistendahl 64-91* (BHO).
Stachys sylvatica L.—U.S.A., Ohio, Athens (cultivated), *Cantino 1364* (BHO).
Stenogyne haliakalae Wawra—U.S.A., Hawaii, Maui, Haleakala National Park, *Olson 5* (K).
Stenogyne kamehamehae Wawra—U.S.A., Hawaii, Molokai, *Degener 5414* (K).
Stenogyne purpurea H. Mann—U.S.A., Hawaii, Kauai, *Degener et al. 23907* (K).
Sulaimania otostegioides (Prain) Hedge & Rech. f.—Pakistan, N Wazir, *Duthie 15788* (K).
Suzukia luchuensis Kudo—Japan, Ryukyu Province, Yaeyama Islands, *Furuse 3205* (K).
Synandra hispidula (Michaux) Baillon—U.S.A, Ohio, Morgan County, *Cantino 1151* (BHO); Lawrence County, *Hammer 6* (BHO).
Thuspeinanta persica (Boiss.) Briq.—Afghanistan, *Aitchison 207* (GH).
Wiedemannia orientalis Fischer & C. Meyer—Turkey, Elazig Province, *Davis & Hedge 28929* (A); Ankara, *Kuntay 48* (MO).

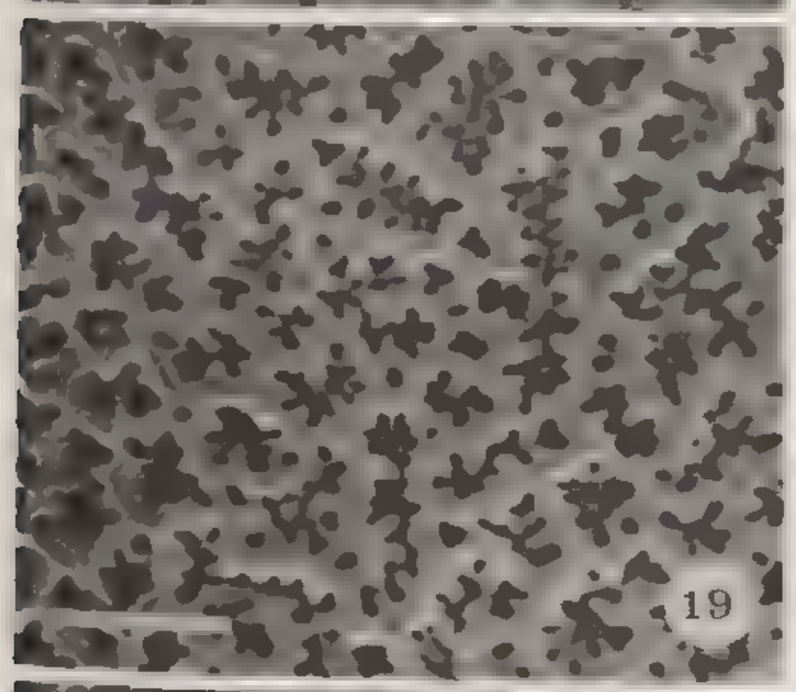


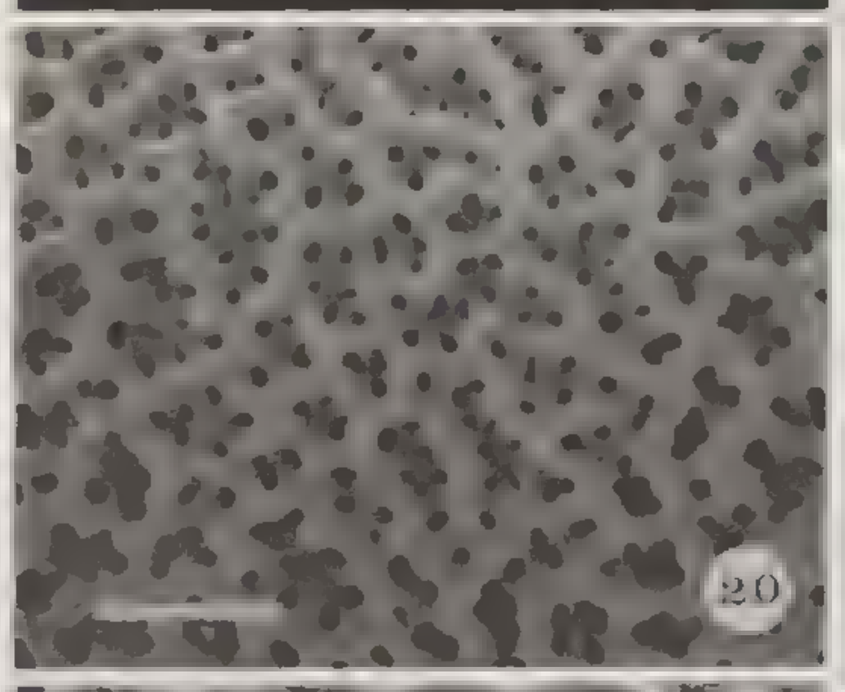
FIGURES 1–15. Pollen of Lamioideae: *Achyrospermum*, *Acrotome*, *Ajugoides*, and *Alajja*. —1, 2. *Achyrospermum aethiopicum*. 3. *Achyrospermum carvalhi*. 4. *Achyrospermum cryptanthum*. —5. *Achyrospermum densiflorum*. 6, 7. *Achyrospermum parviflorum*.—8, 9. *Achyrospermum schimperi*.—10, 11. *Acrotome angustifolia*.—12, 13. *Ajugoides humilis* (*US 350854*).—14, 15. *Alajja rhomboidea*. Scales = 0.5 μm (4); 1 μm (2, 3, 5, 7, 9, 11, 13, 15); 2.5 μm (1, 8, 10); 5 μm (6, 12, 14).

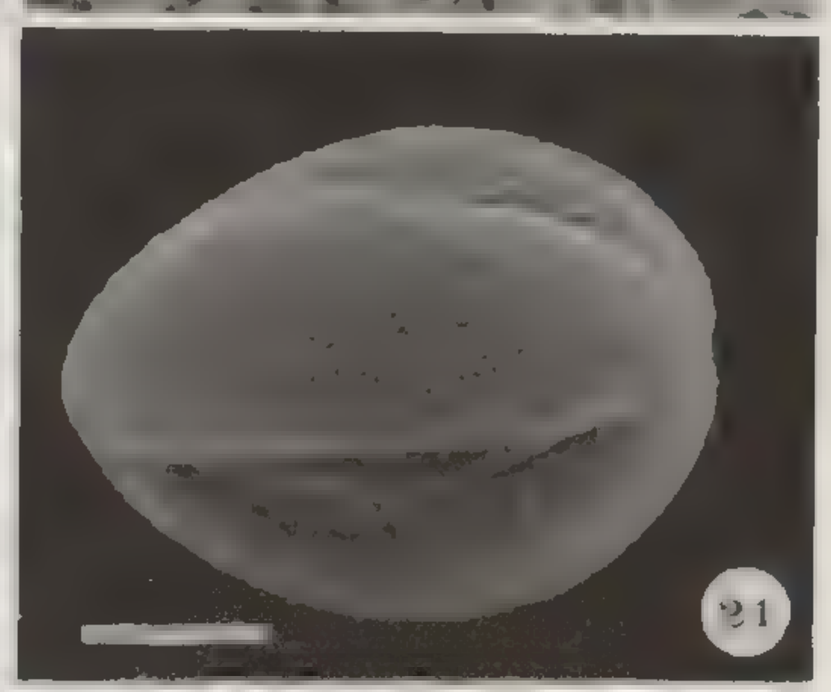


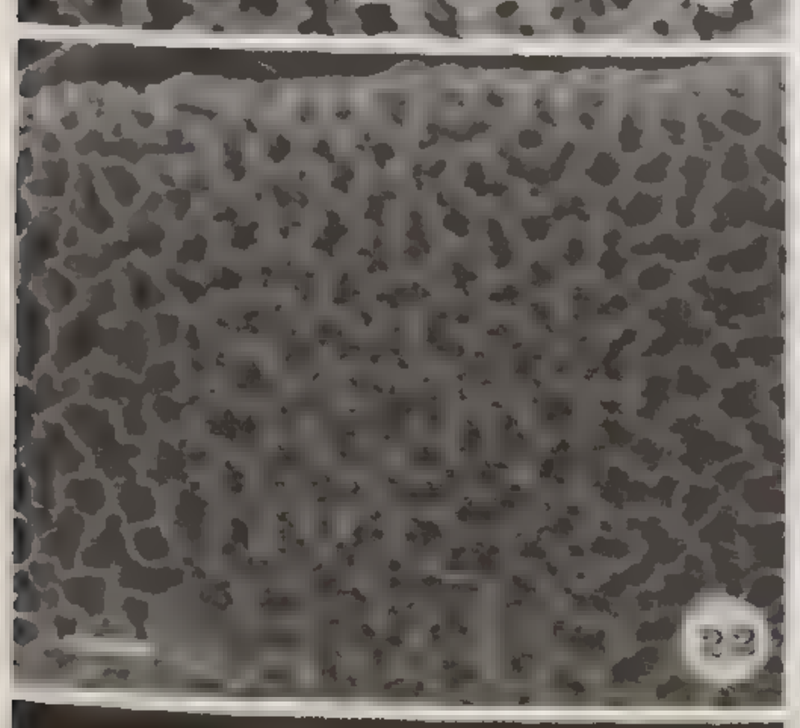


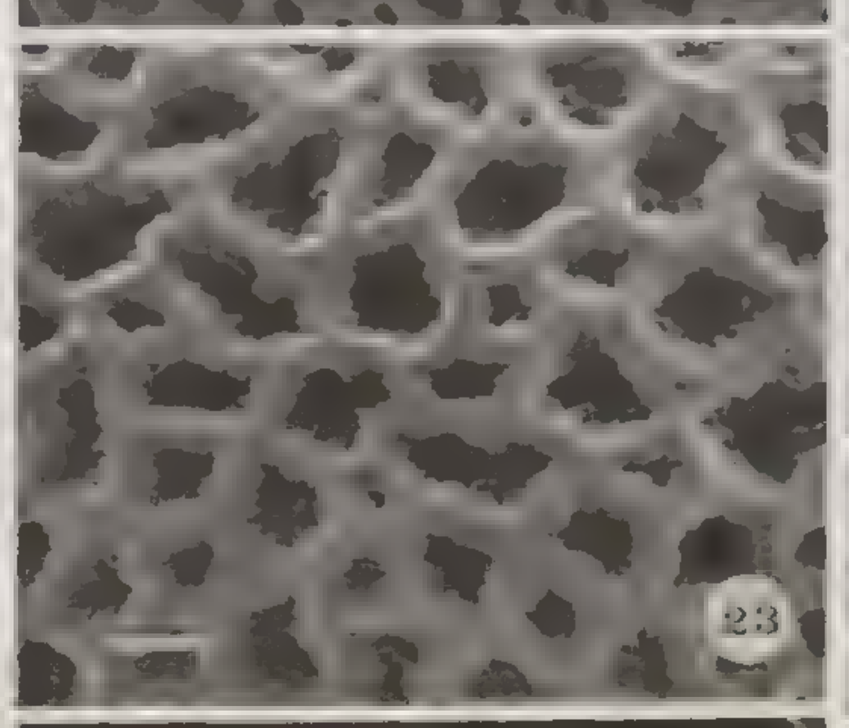


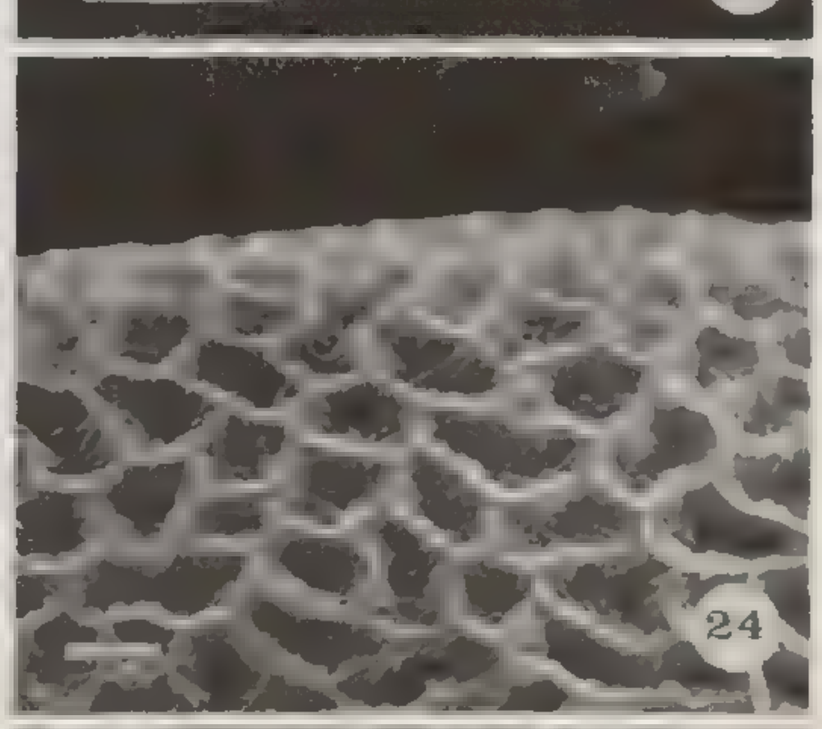


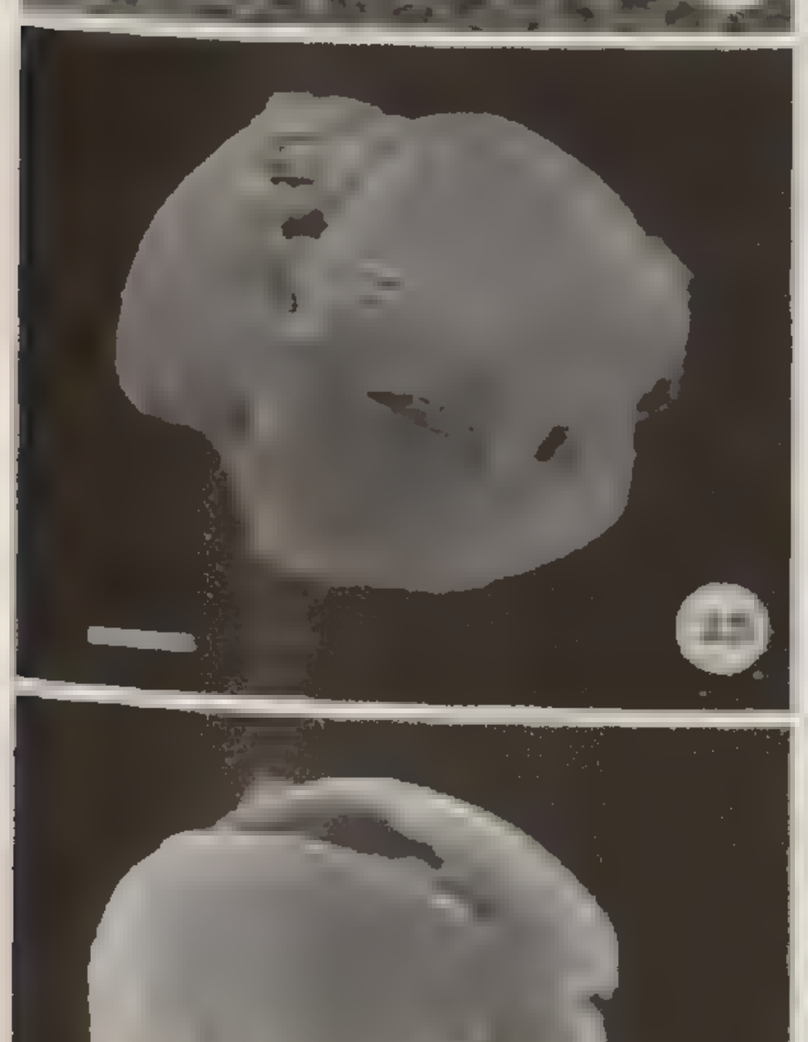


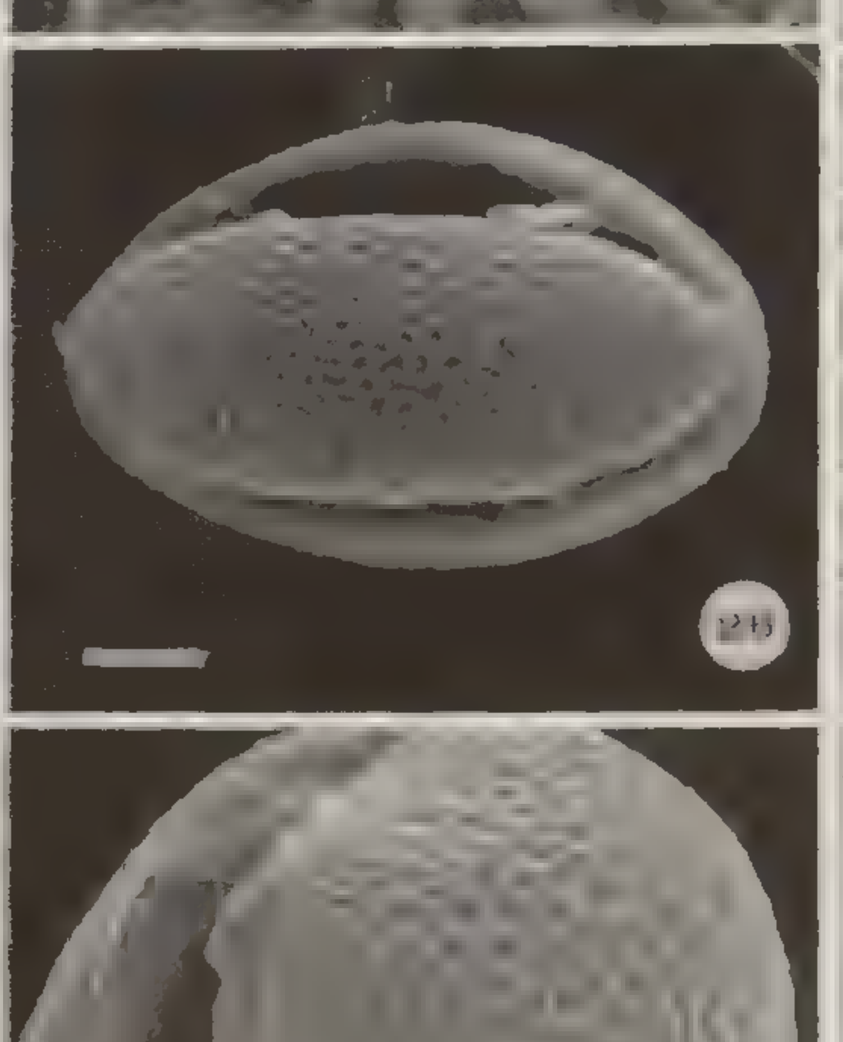


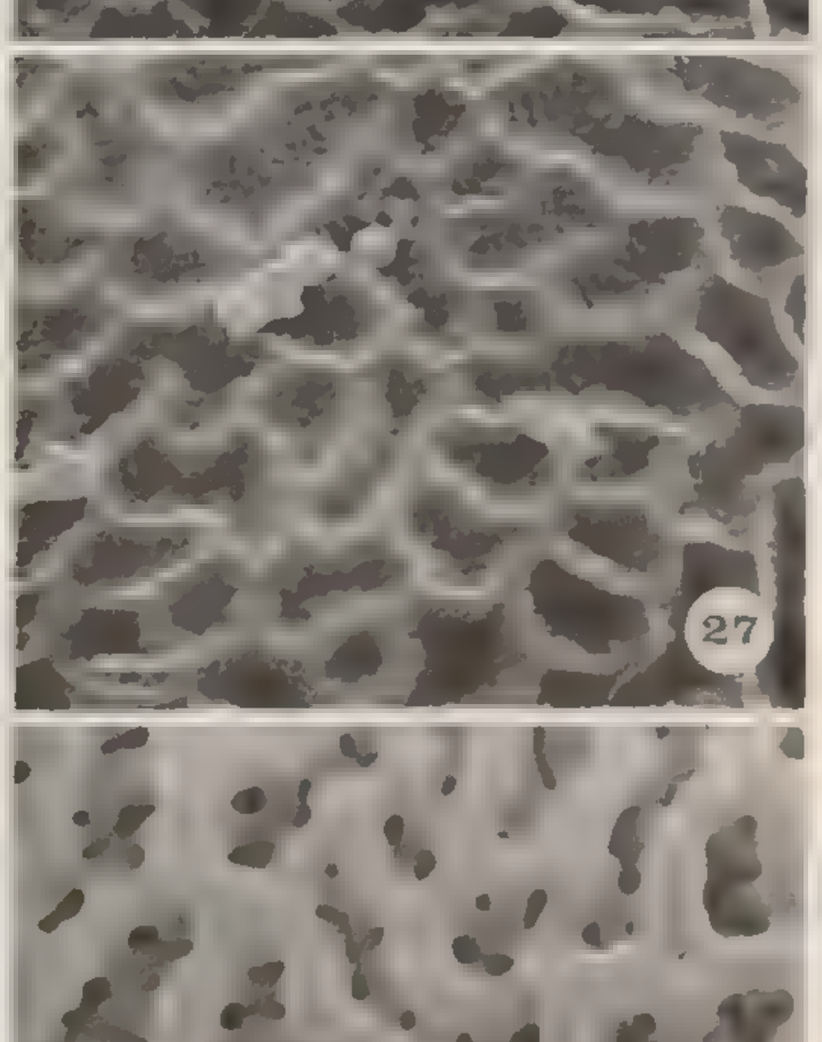




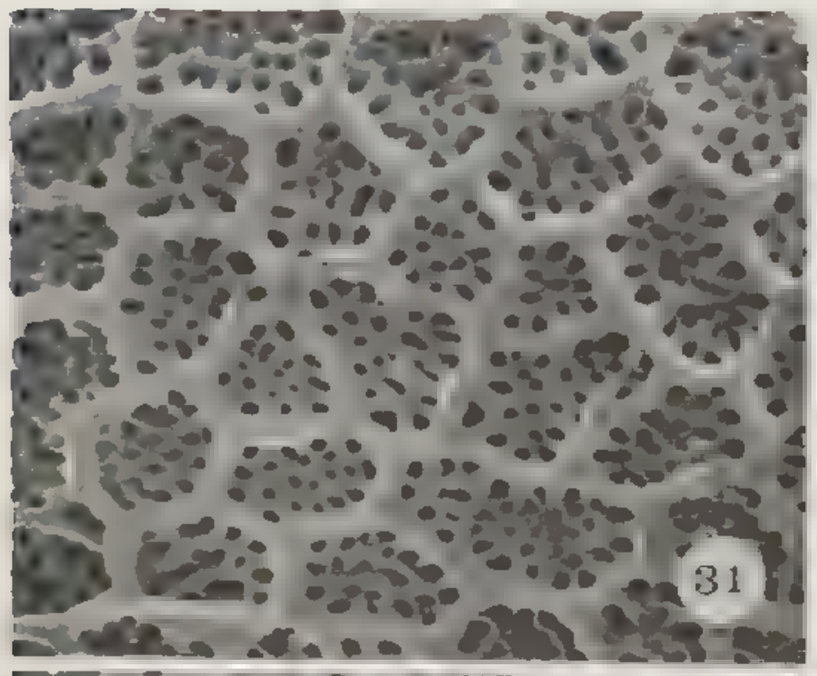


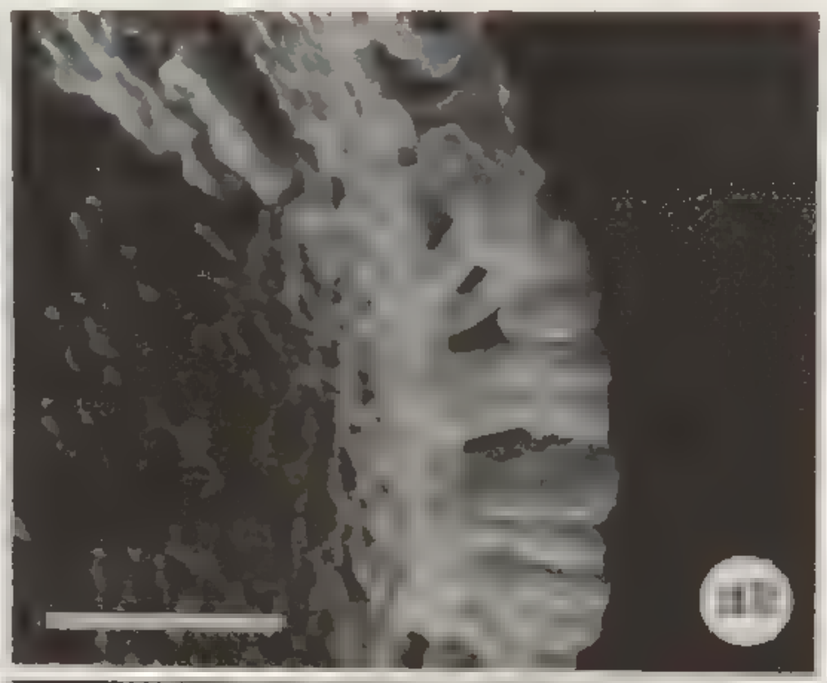


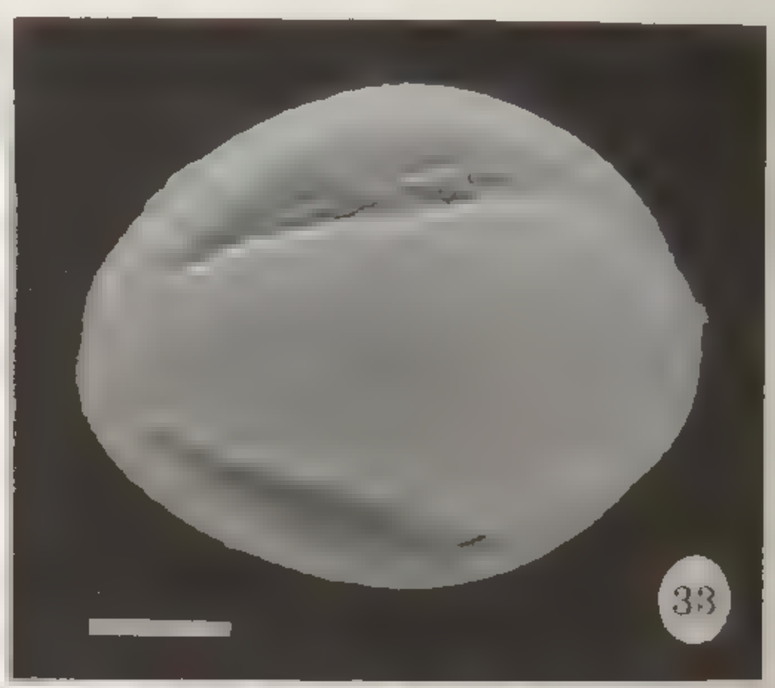


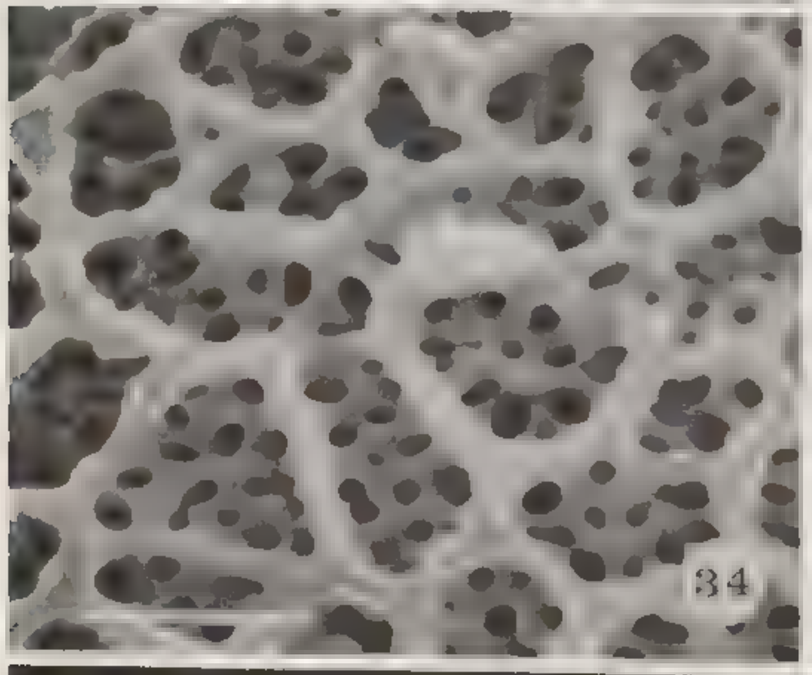


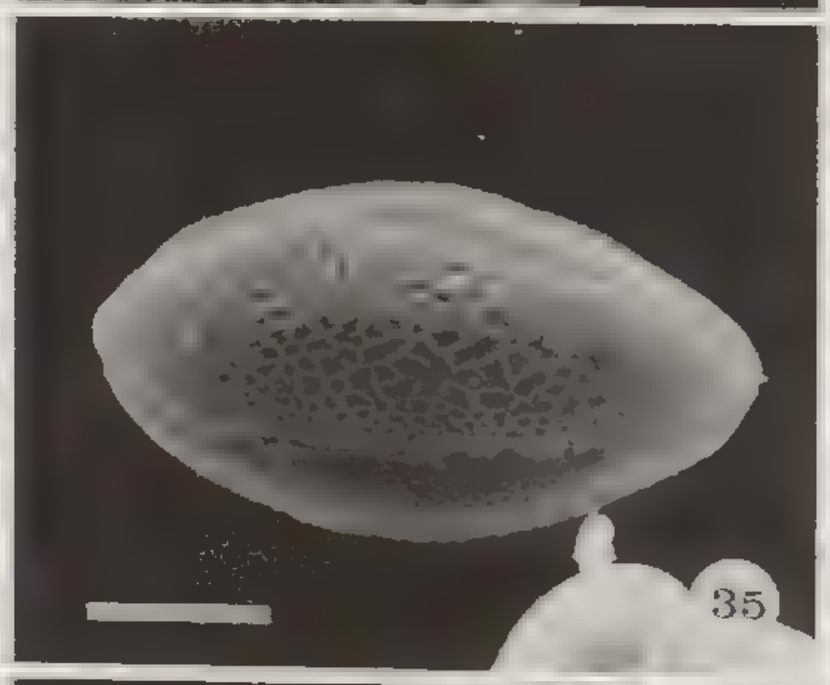
FIGURES 16–30. Pollen of Lamioideae: *Ballota*, *Brazoria*, *Chaiturus*, and *Chamaesphacos*. —16. *Ballota africana*. —17, 18. *Ballota hirsuta*. —19. *Ballota integrifolia*. —20. *Ballota nigra* (*Larsen et al. 35996*). —21, 22. *Ballota pseudodictamnus*. —23. *Brazoria arenaria*. —24. *Brazoria pulcherrima*. —25. *Brazoria scutellarioides* (*Tharp s.n.*). —26, 27. *Brazoria truncata* (*Correll & Ogden 25300*). —28, 29. *Chaiturus marrubiastrum*. —30. *Chamaesphacos ilicifolius*. Scales = 1 μm (16, 18, 19, 20, 22, 23, 24, 27, 30); 2.5 μm (17, 29); 5 μm (21, 25, 26); 10 μm (28).

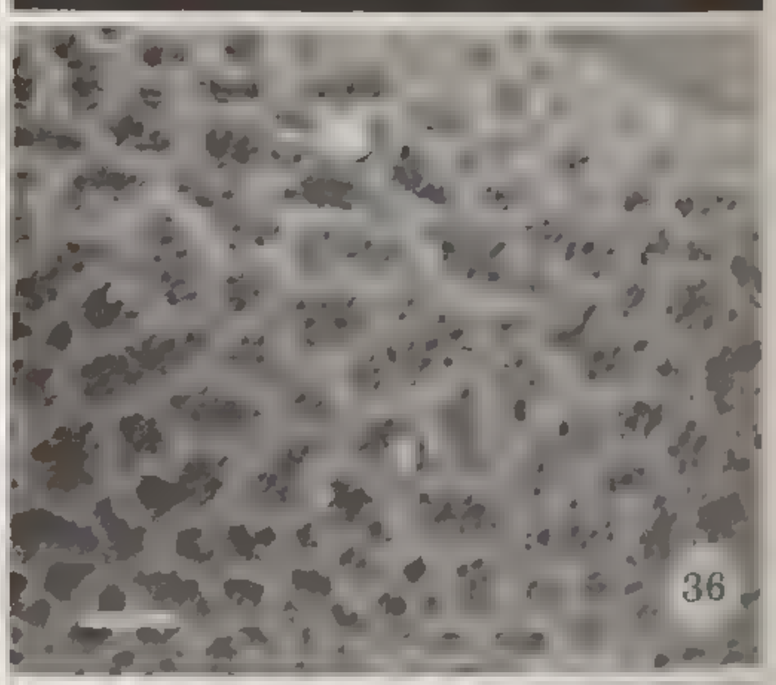


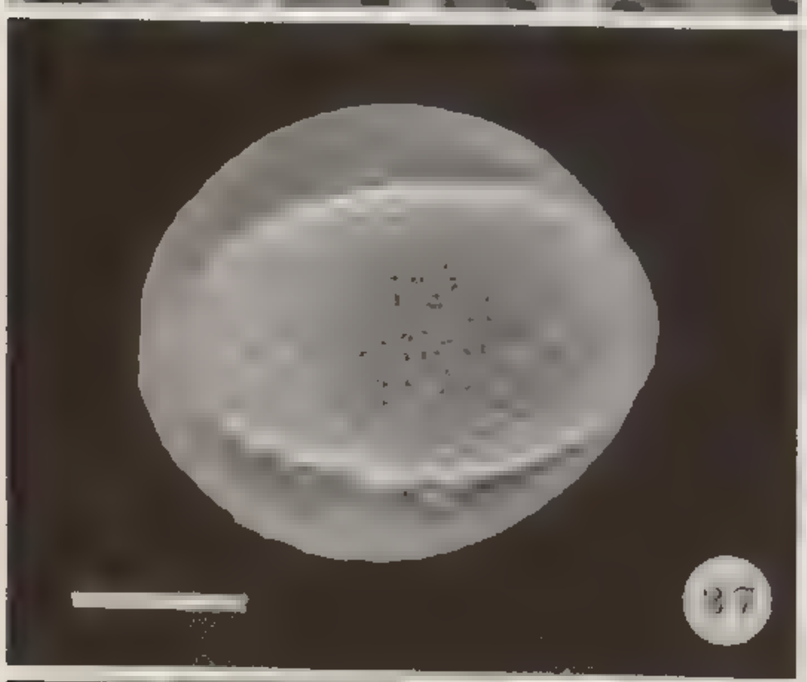


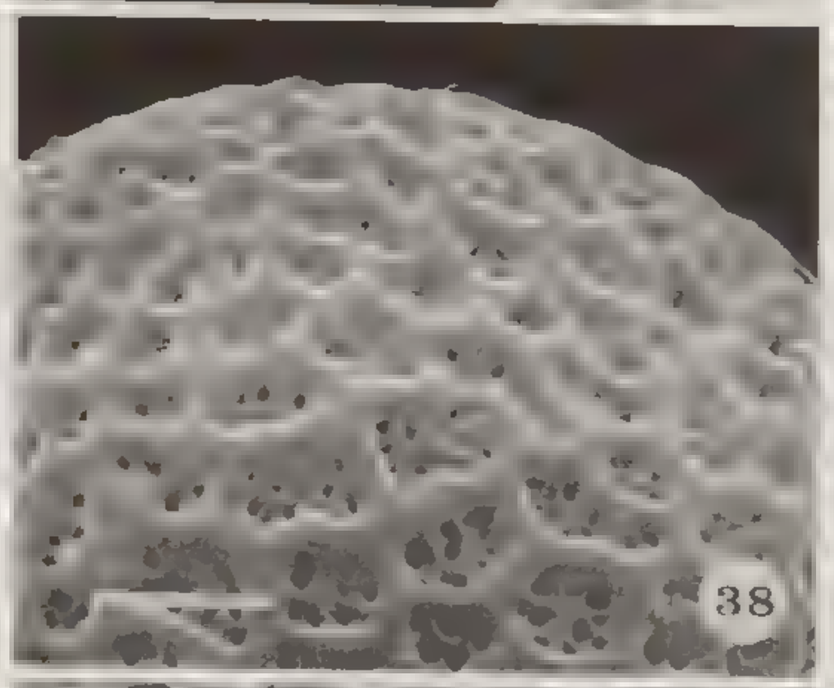


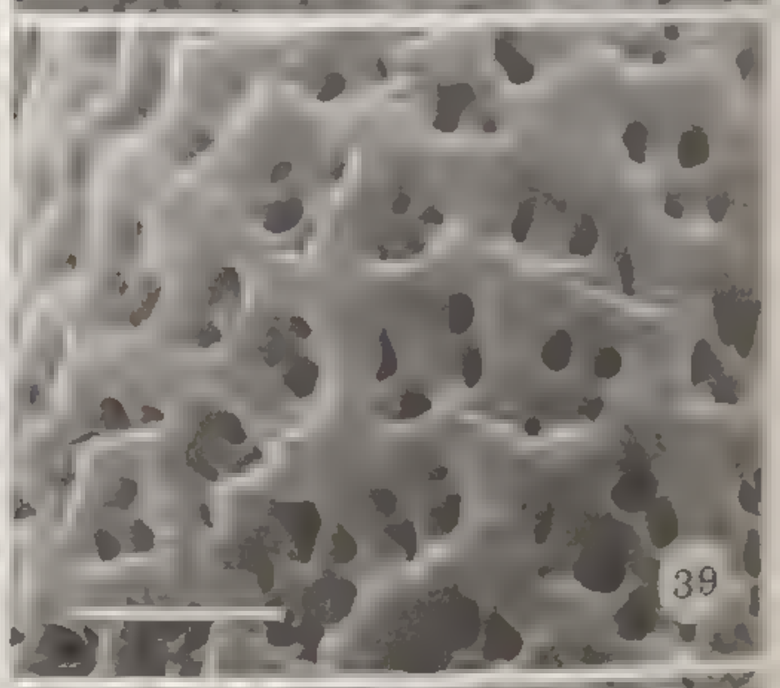


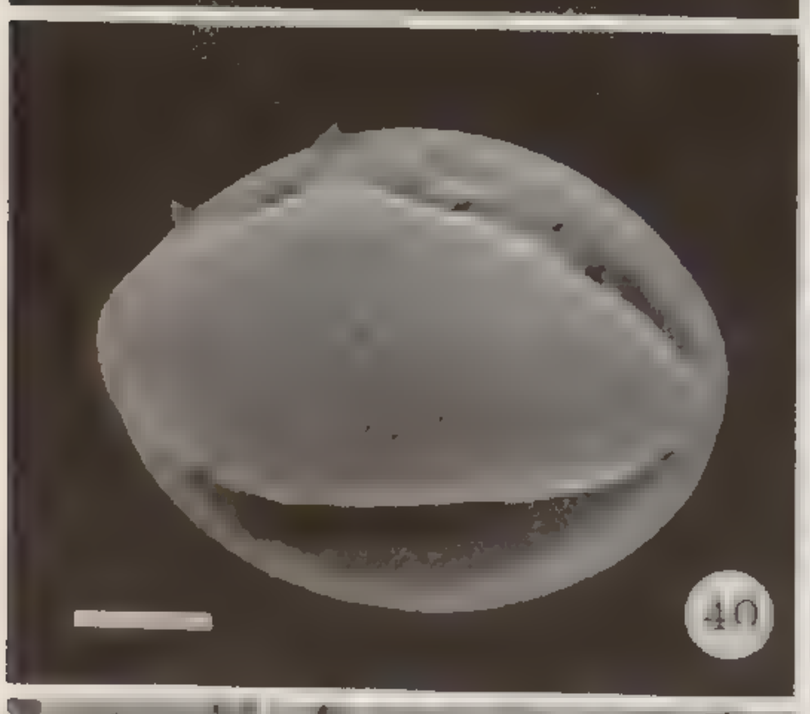


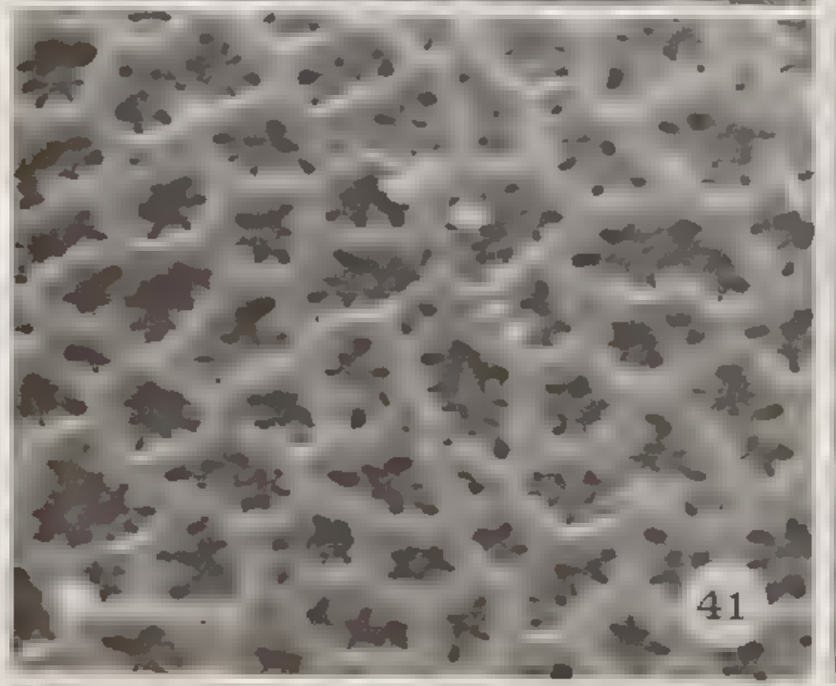


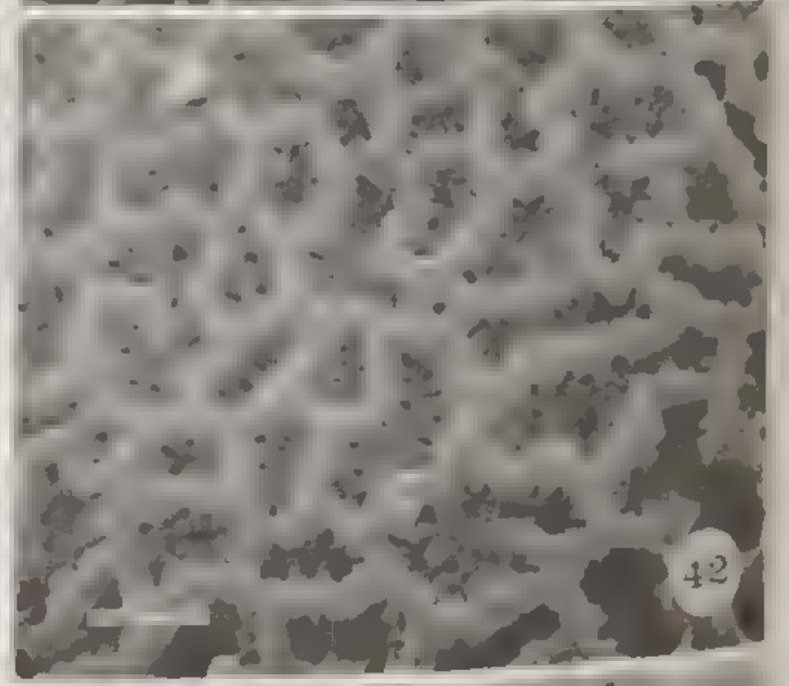


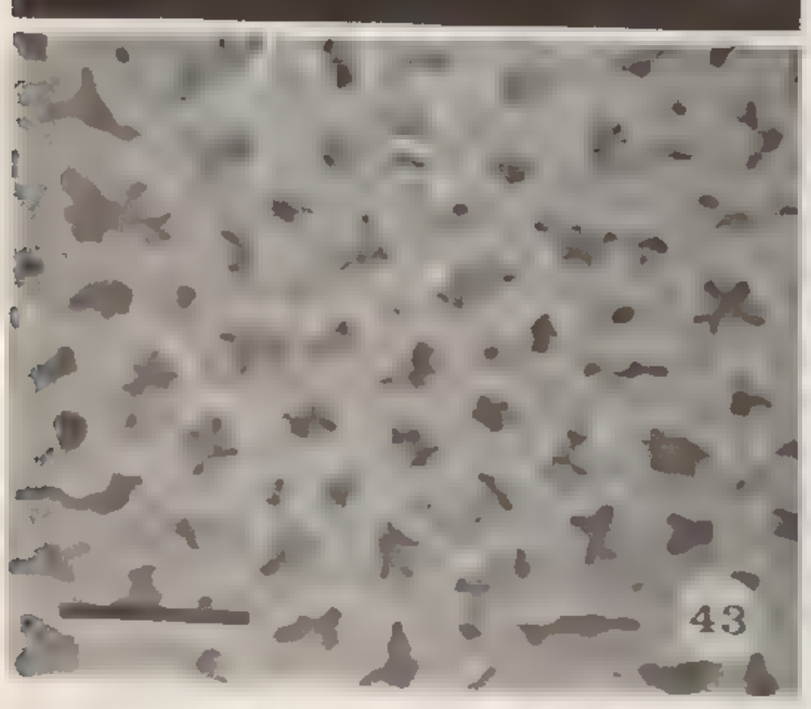


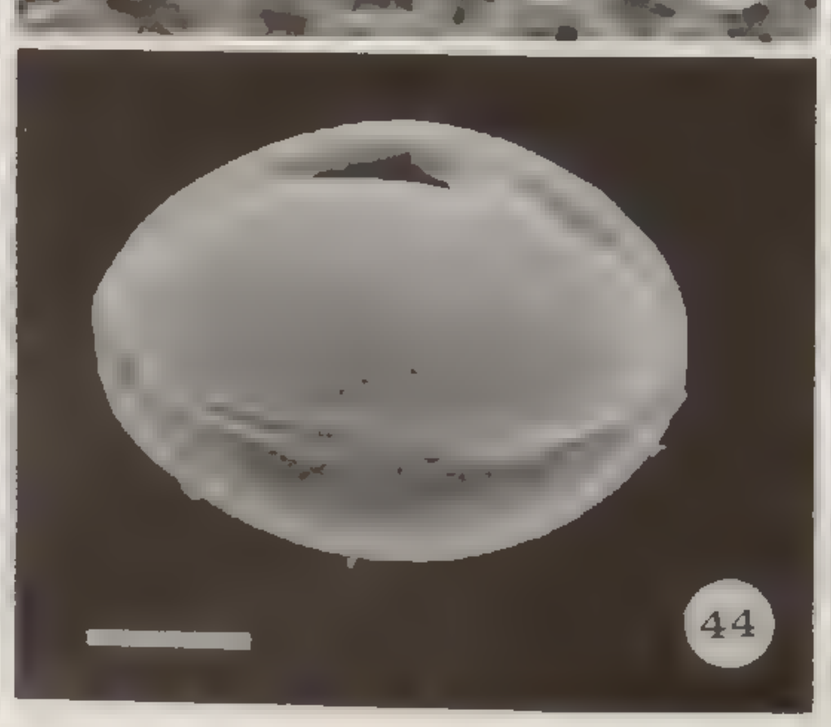


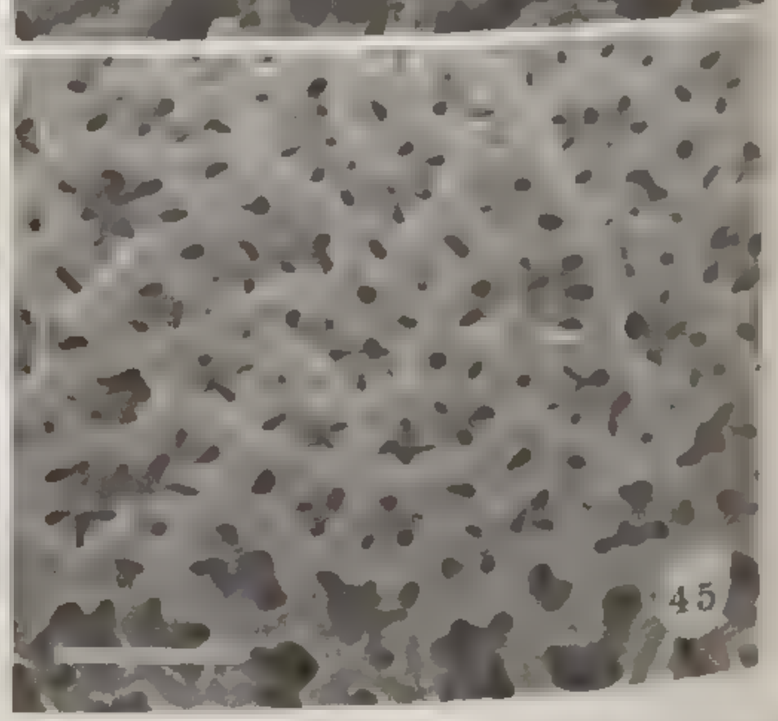




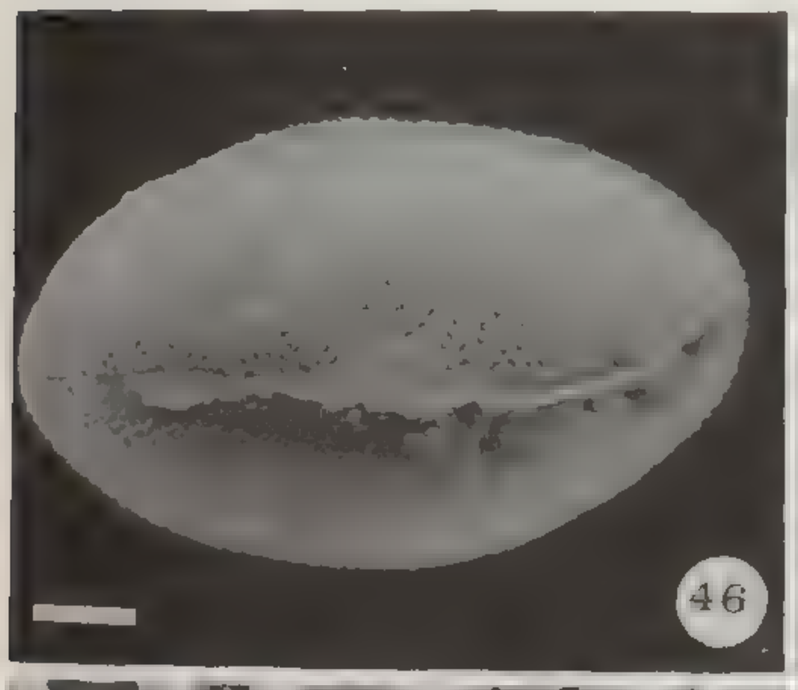


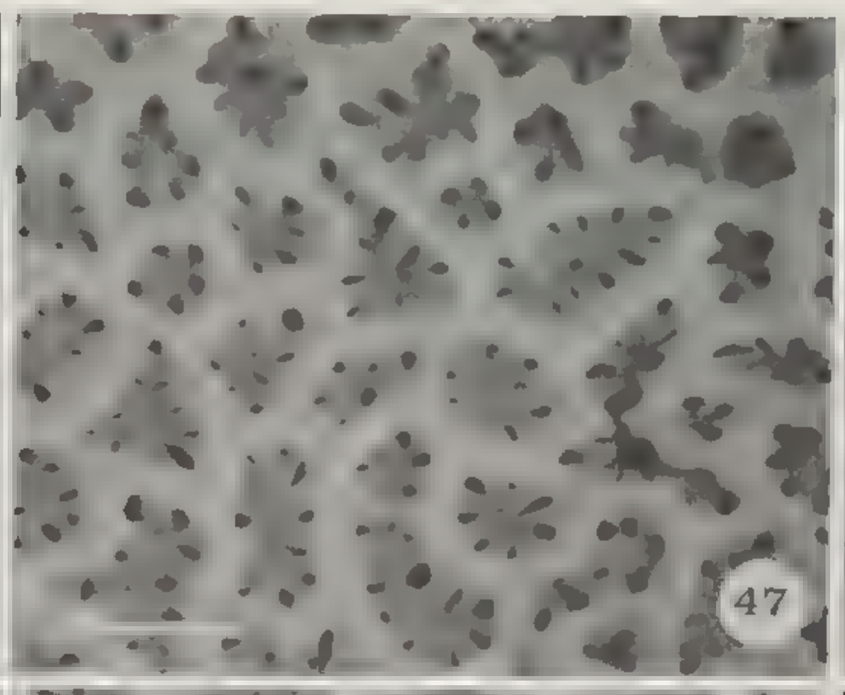


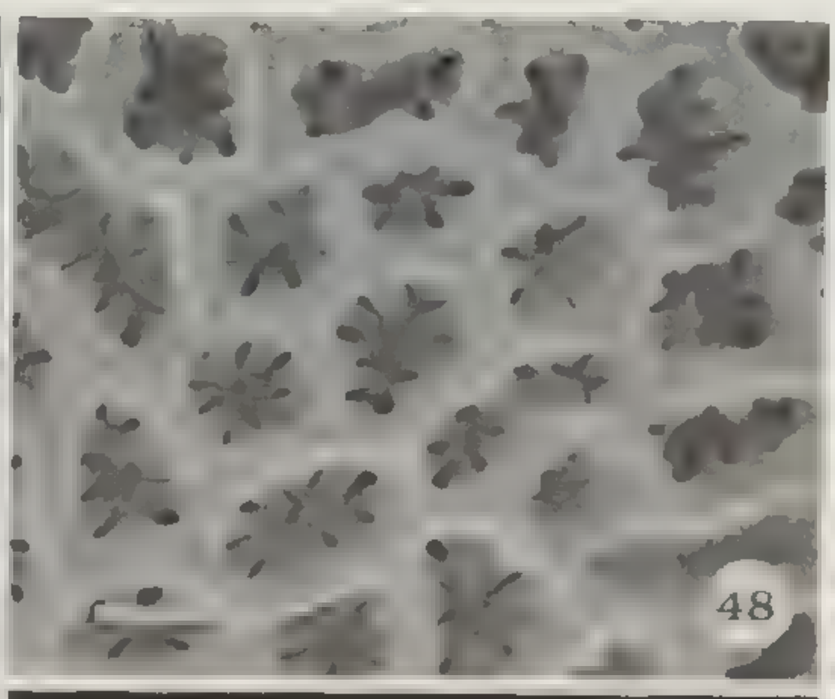


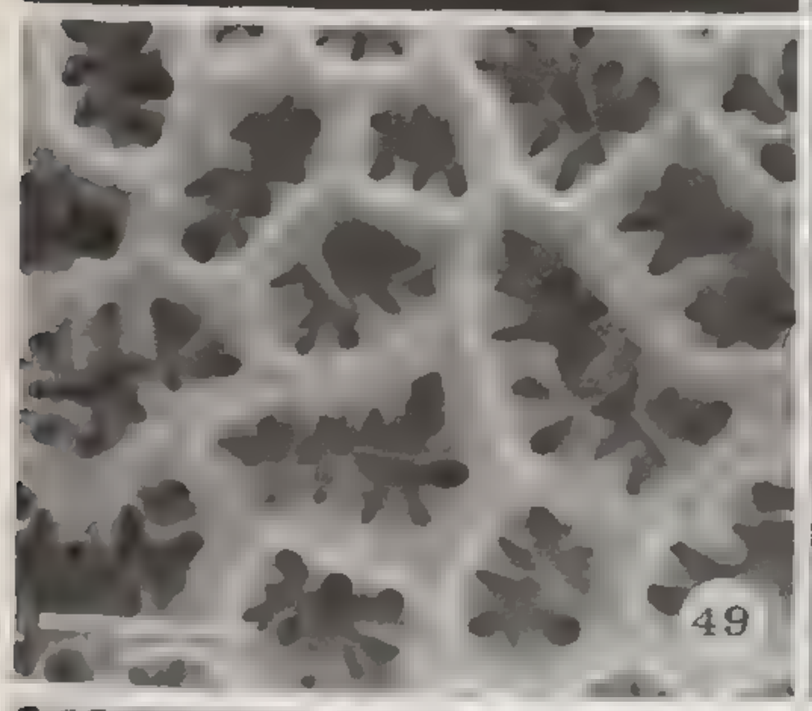


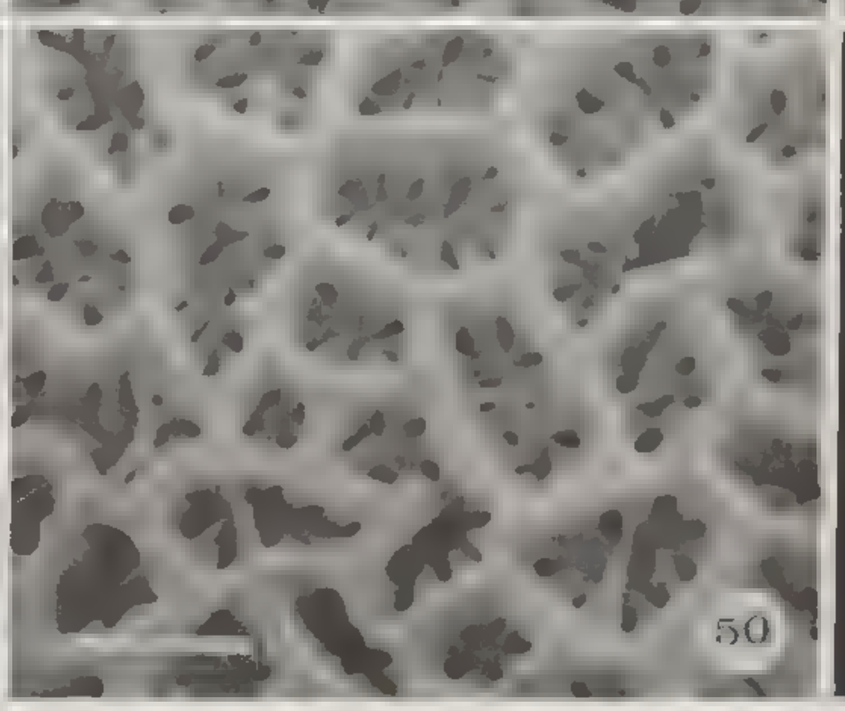
FIGURES 31–45. Pollen of Lamioideae: *Chelonopsis*, *Colquhounia*, *Craniotome*, *Eremostachys*, and *Eriophyton*. —31, 32. *Chelonopsis lichiangensis*. —33, 34. *Chelonopsis odontochila*. —35, 36. *Colquhounia seguinii*. —37, 38. *Craniotome furcata* (*Polunin et al. 1297*). —39. *Craniotome furcata* (*Banerjo 2864*). —40, 41. *Eremostachys iliensis*. —42. *Eremostachys rotata*. —43. *Eremostachys speciosa*. —44, 45. *Eriophyton wallichianum*. Scales = 1 μm (31, 32, 34, 36, 38, 39, 41, 42, 43, 45); 5 μm (33, 35, 37, 40, 44).

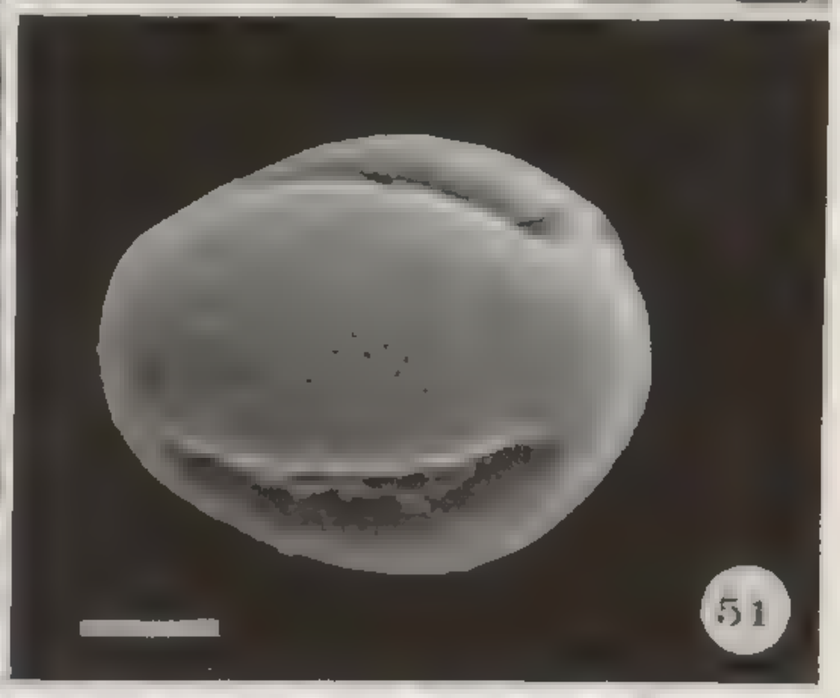


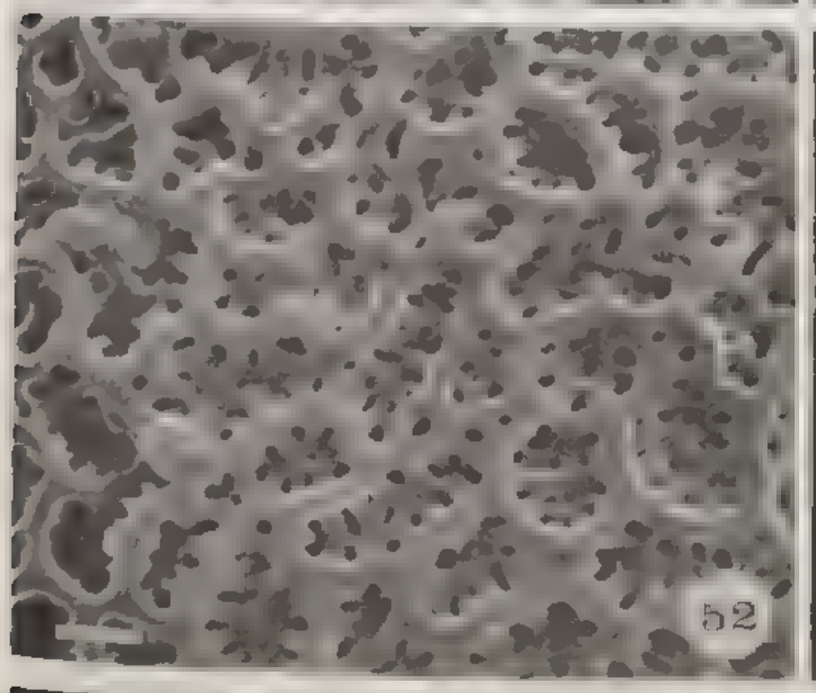


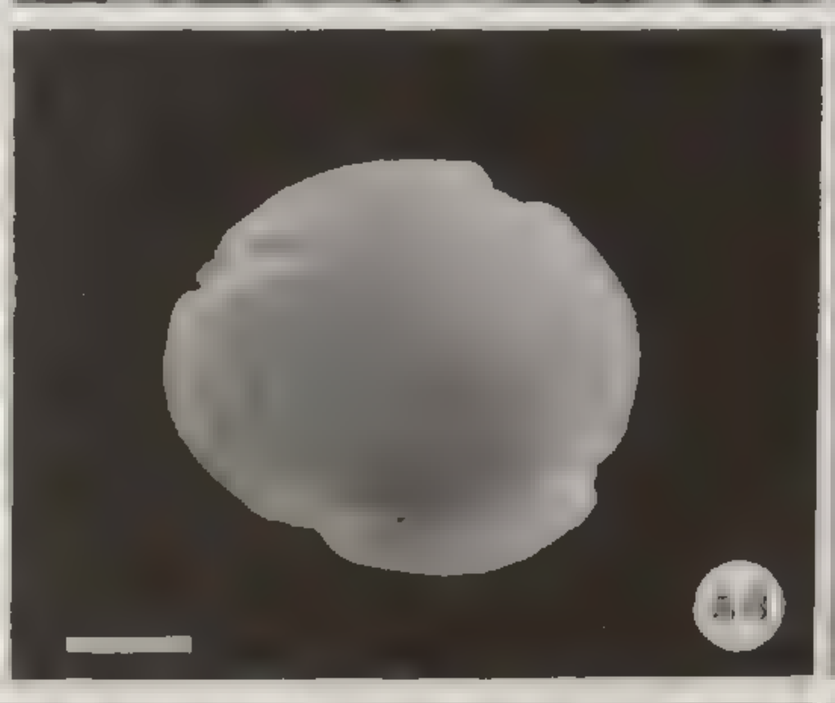


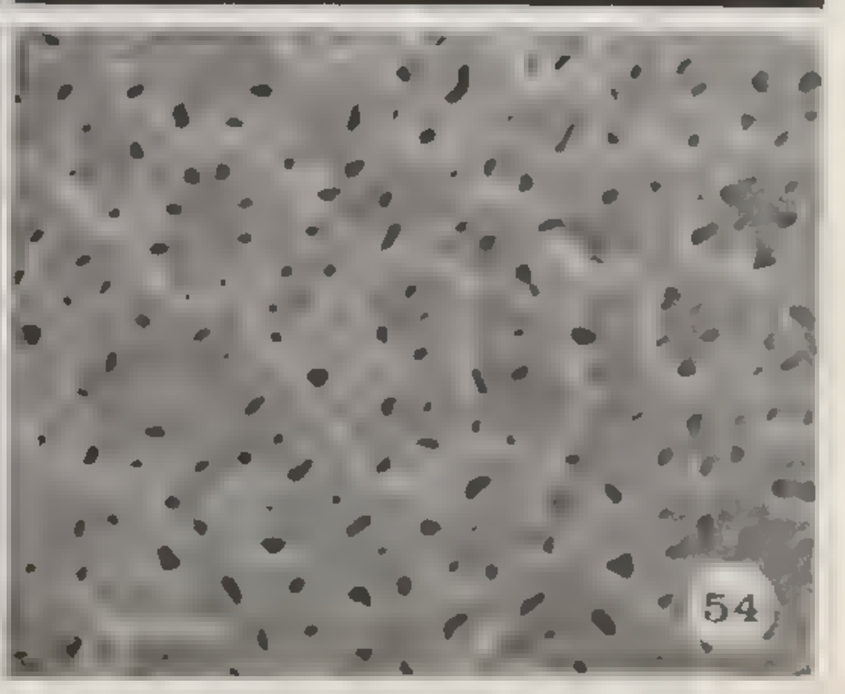


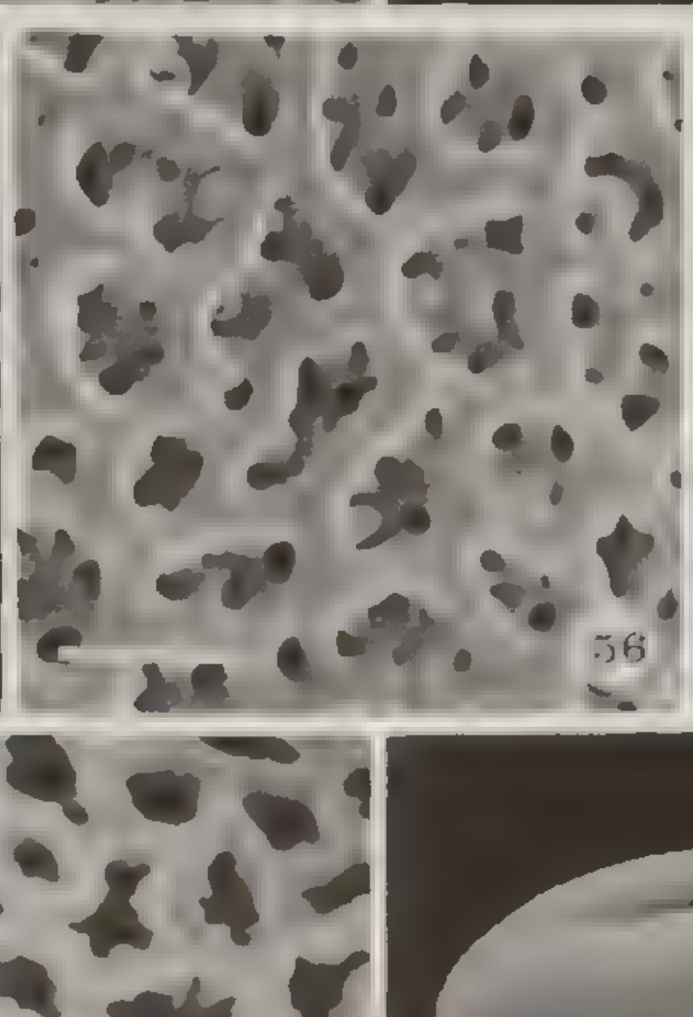


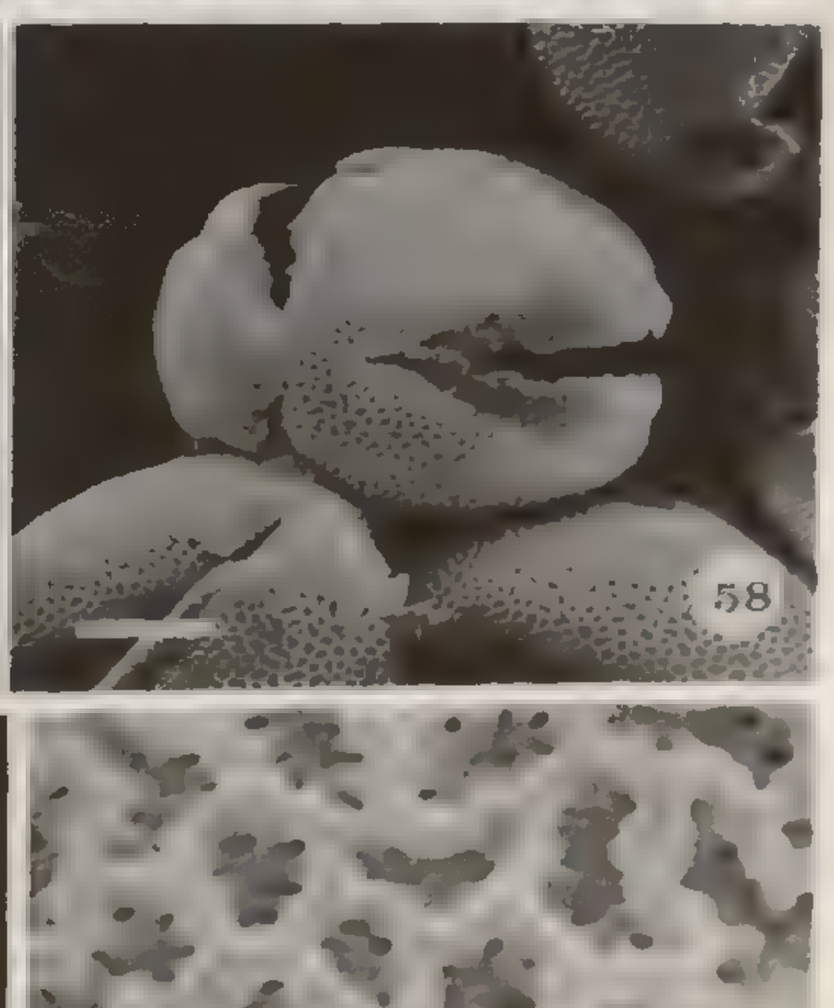


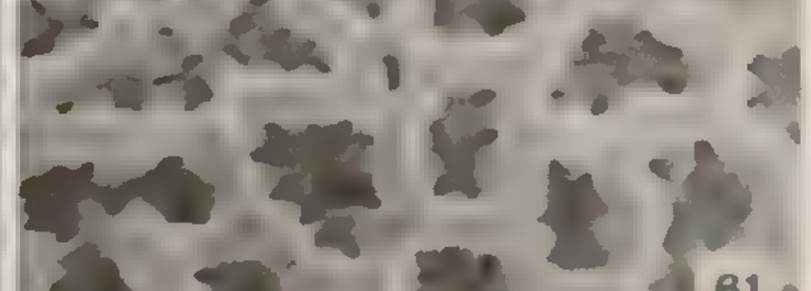






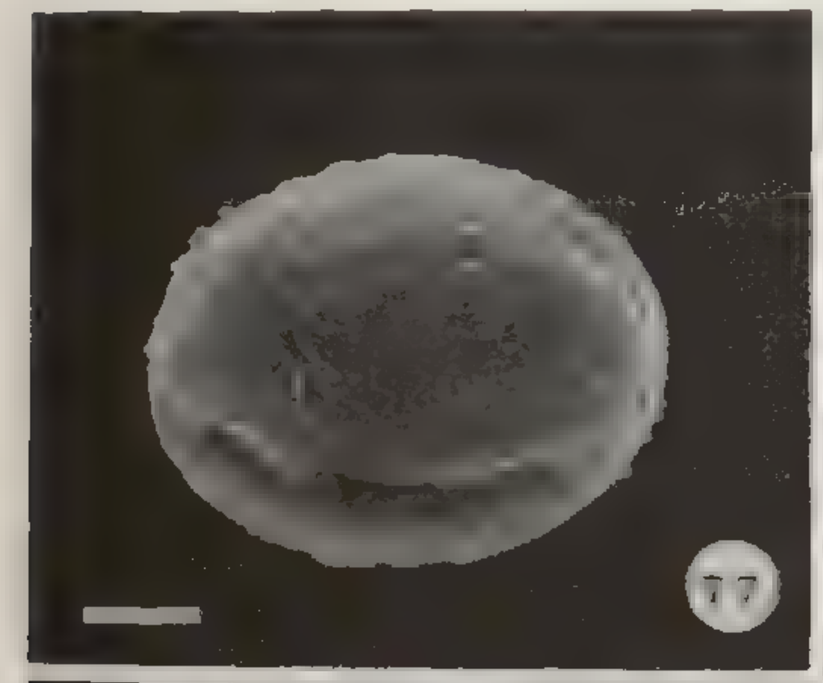


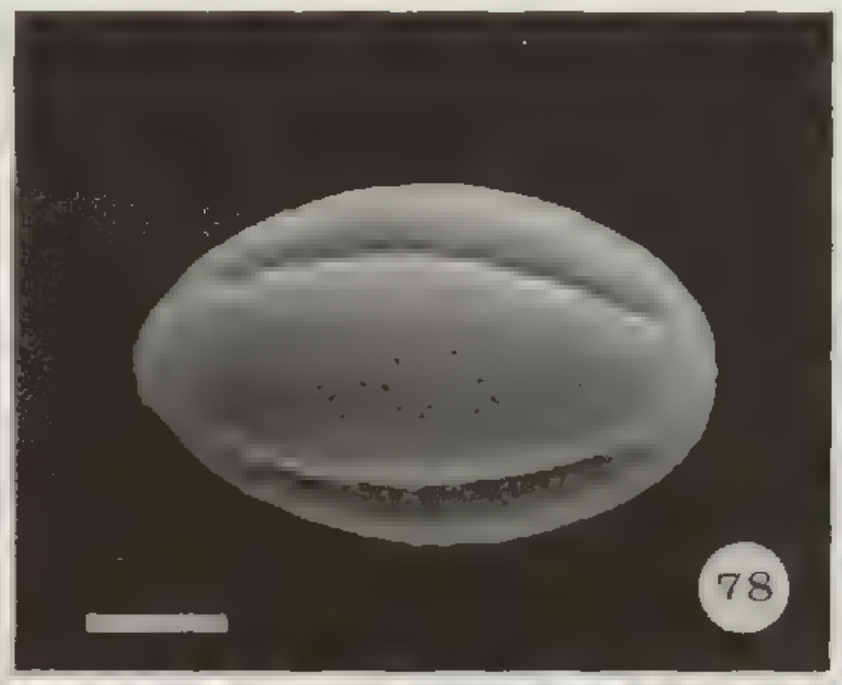


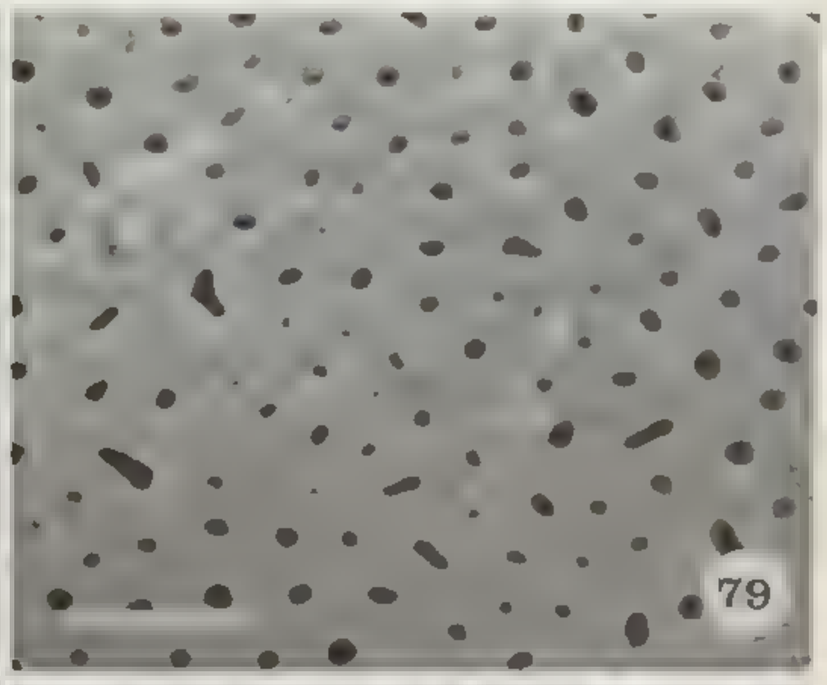


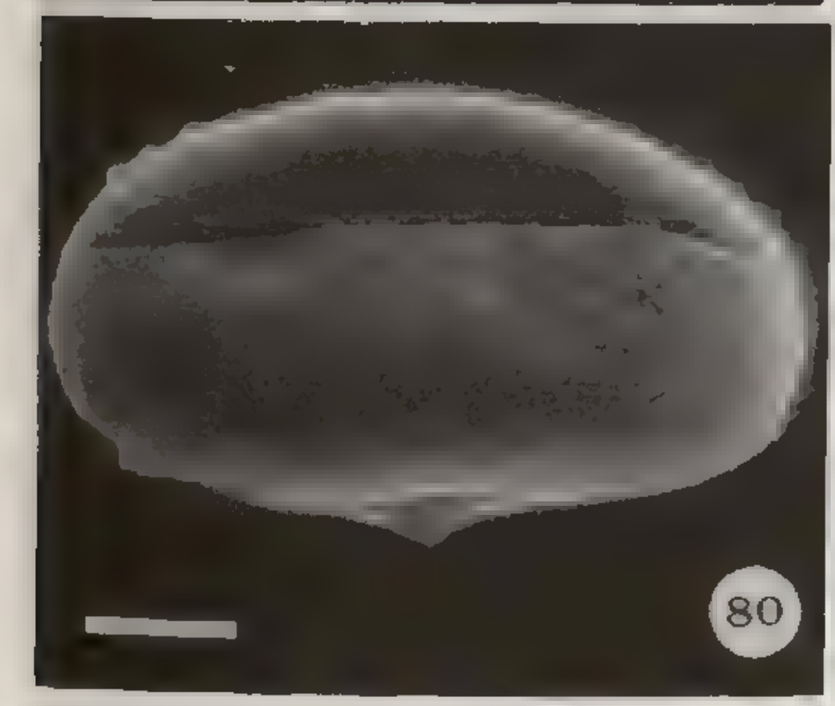
FIGURES 46–61. Pollen of Lamioideae: *Galeopsis*, *Haplostachys*, *Hypogomphia*, and *Lagochilus*.—46, 47. *Galeopsis bifida*. 48. *Galeopsis pubescens*. 49. *Galeopsis speciosa*. 50. *Galeopsis tetrahit*.—51, 52. *Haplostachys haplostachya*. 53, 54. *Haplostachys linearifolia*. 55–57. *Hypogomphia turkestana* (*Hewer 1025A*).—58, 59. *Lagochilus aucheri*. 60, 61. *Lagochilus diacanthophyllus*. Scales = 1 μm (47, 48, 49, 50, 52, 54, 56, 57, 59, 61); 5 μm (46, 55, 58, 60); 10 μm (51, 53).

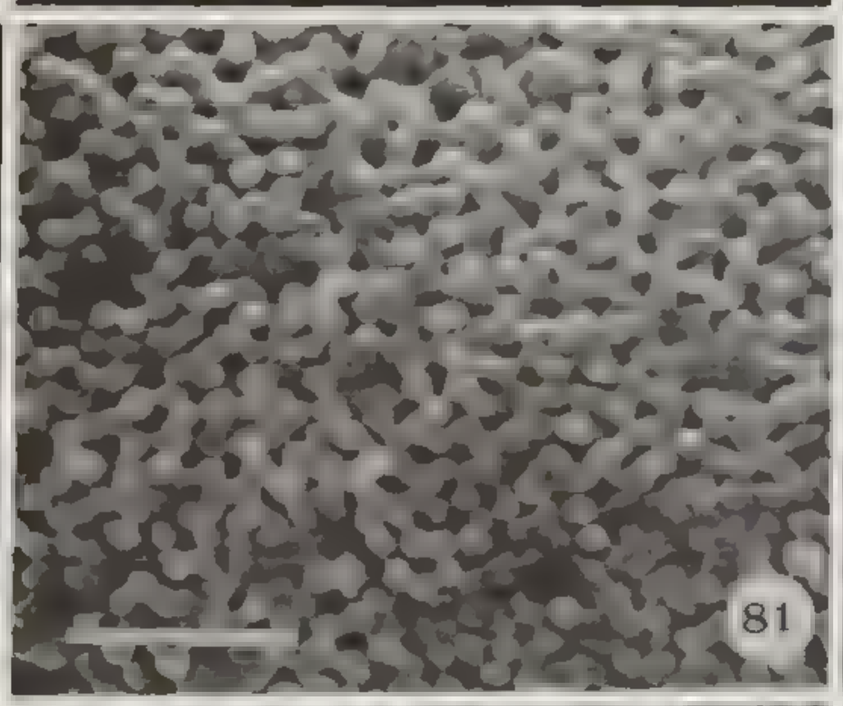
FIGURES 62–76. Pollen of Lamioideae: *Gomphostemma*. —62, 63. *Gomphostemma chinense*. —64–66. *Gomphostemma intermedium*. —67, 68. *Gomphostemma leptodon*. —69, 70. *Gomphostemma javanicum*. —71, 72. *Gomphostemma lucidum*. 73, 74. *Gomphostemma parviflorum*. —75, 76. *Gomphostemma wallichii*. Scales = 0.5 μm (63, 66); 1 μm (65, 68, 70, 72, 74, 76); 5 μm (62, 64, 67, 69, 71, 73, 75).

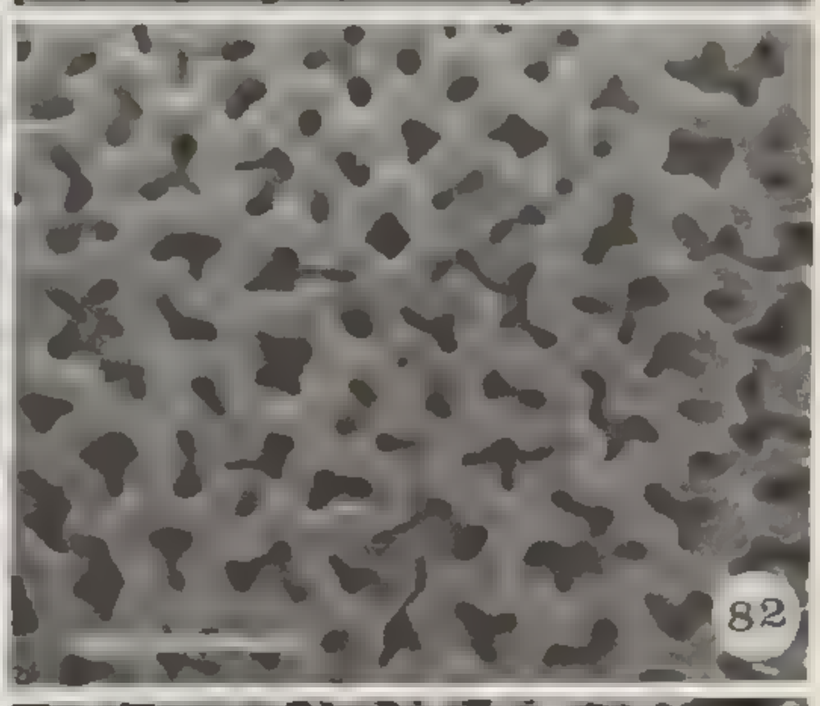


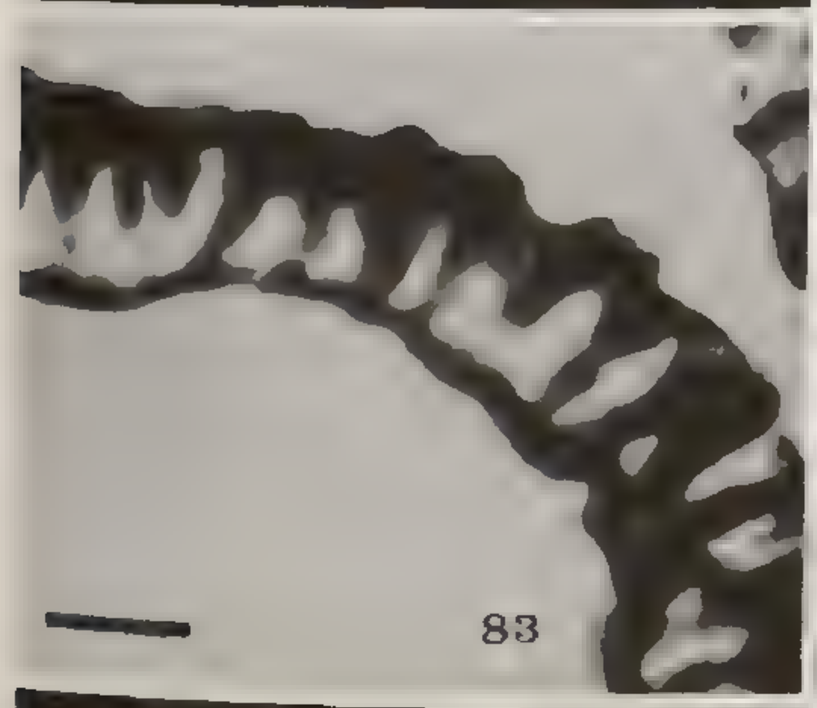


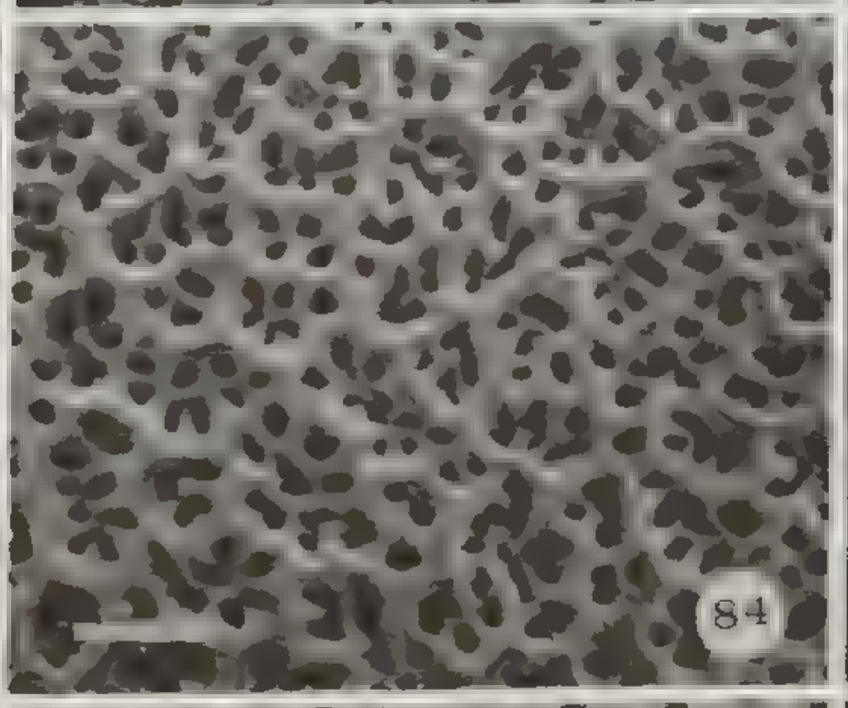


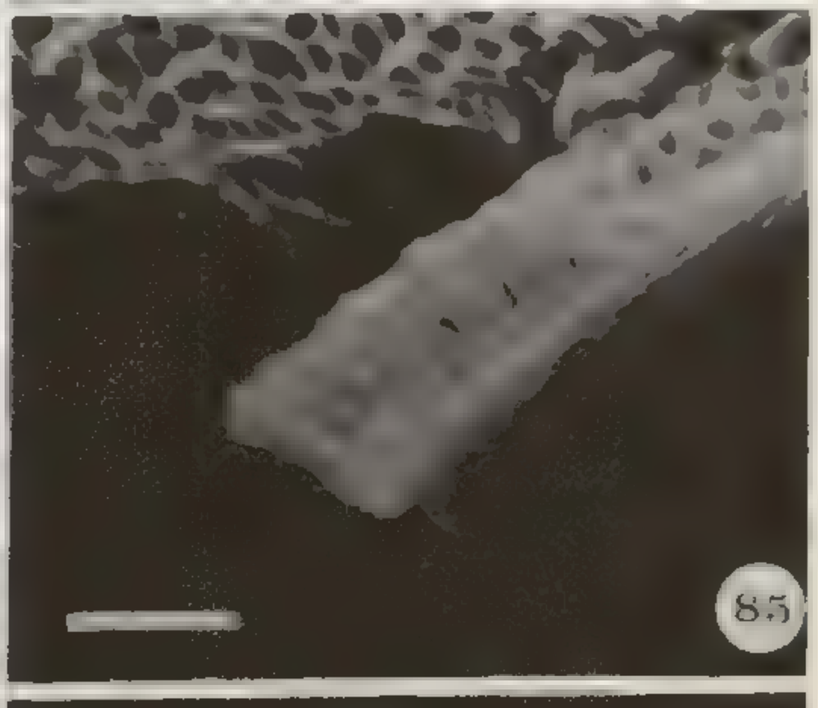


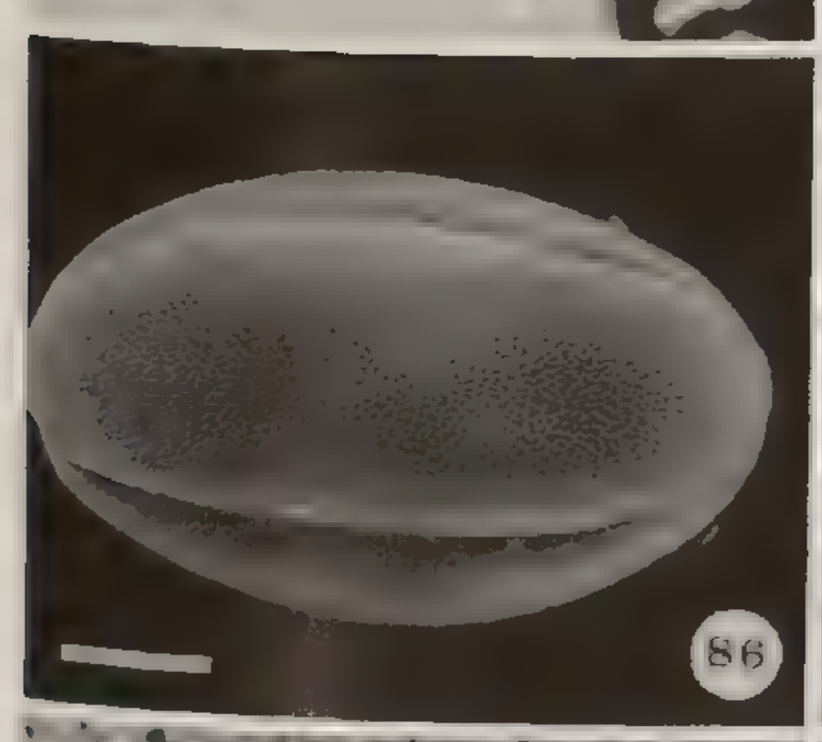


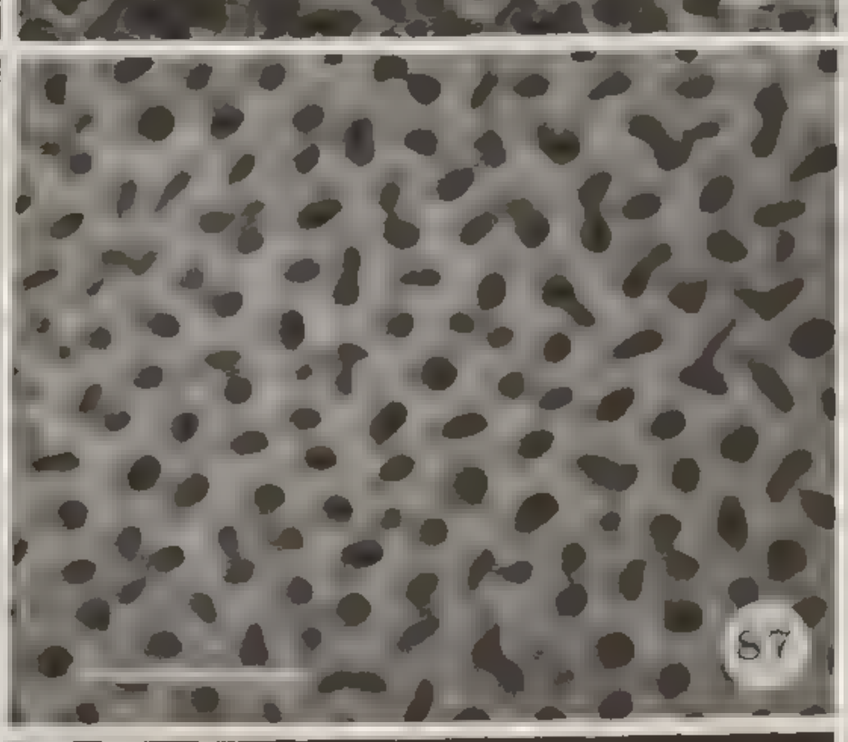


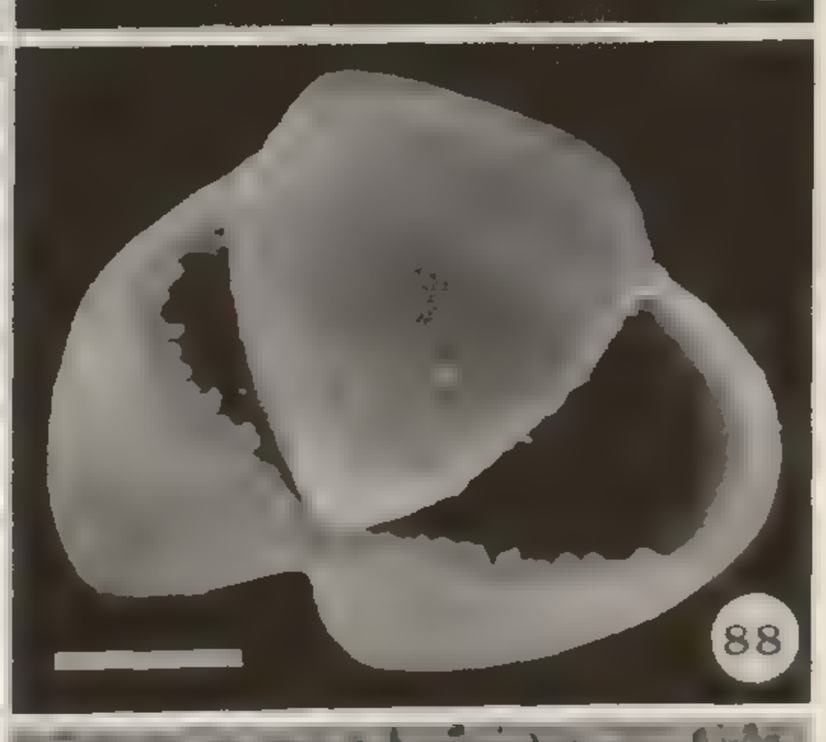


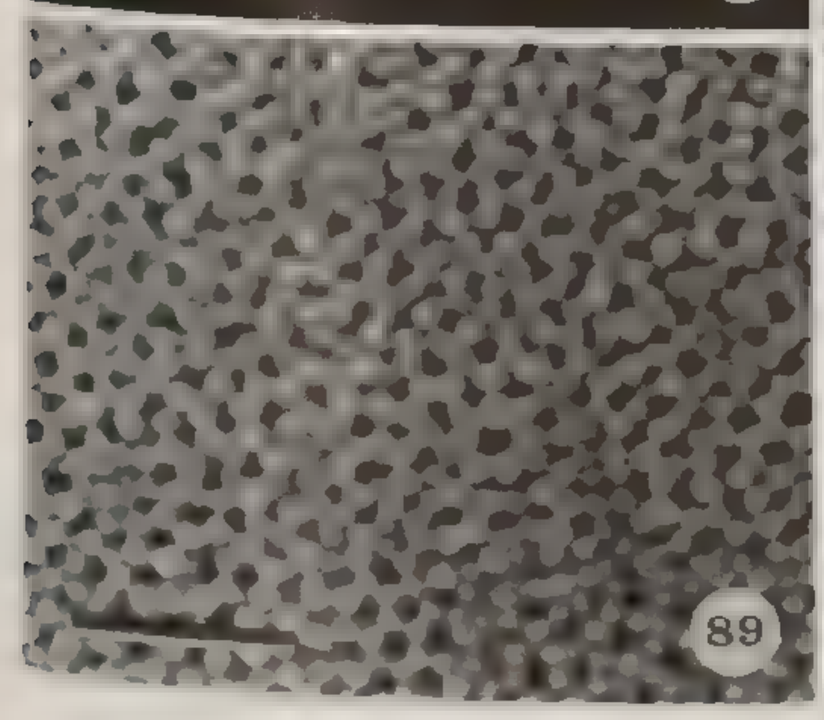


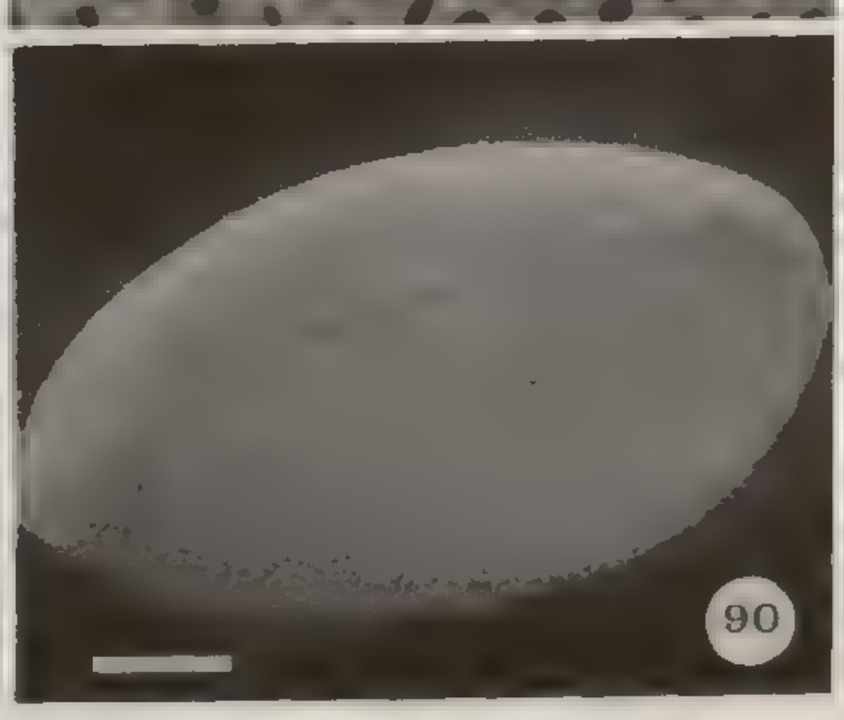


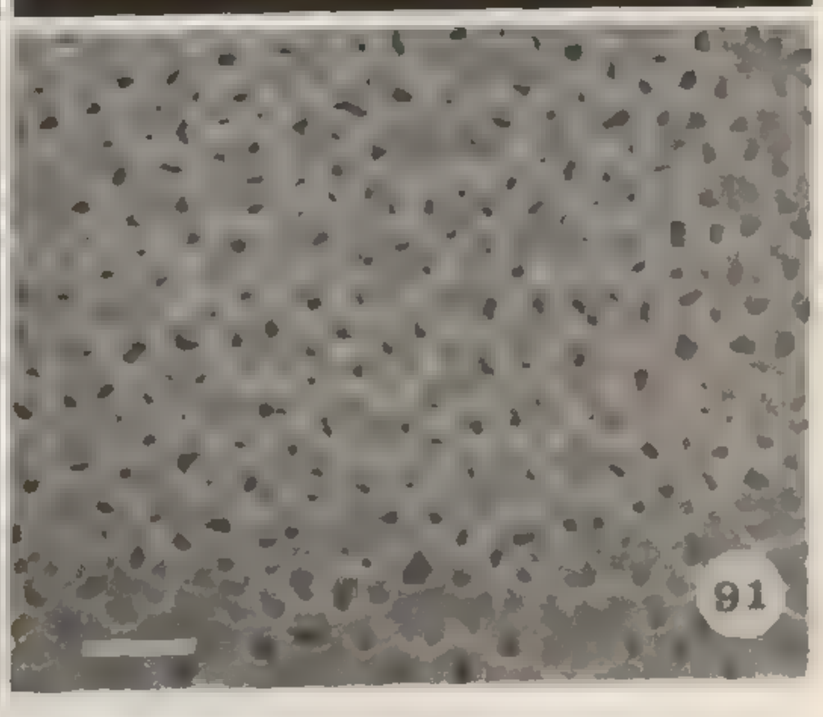






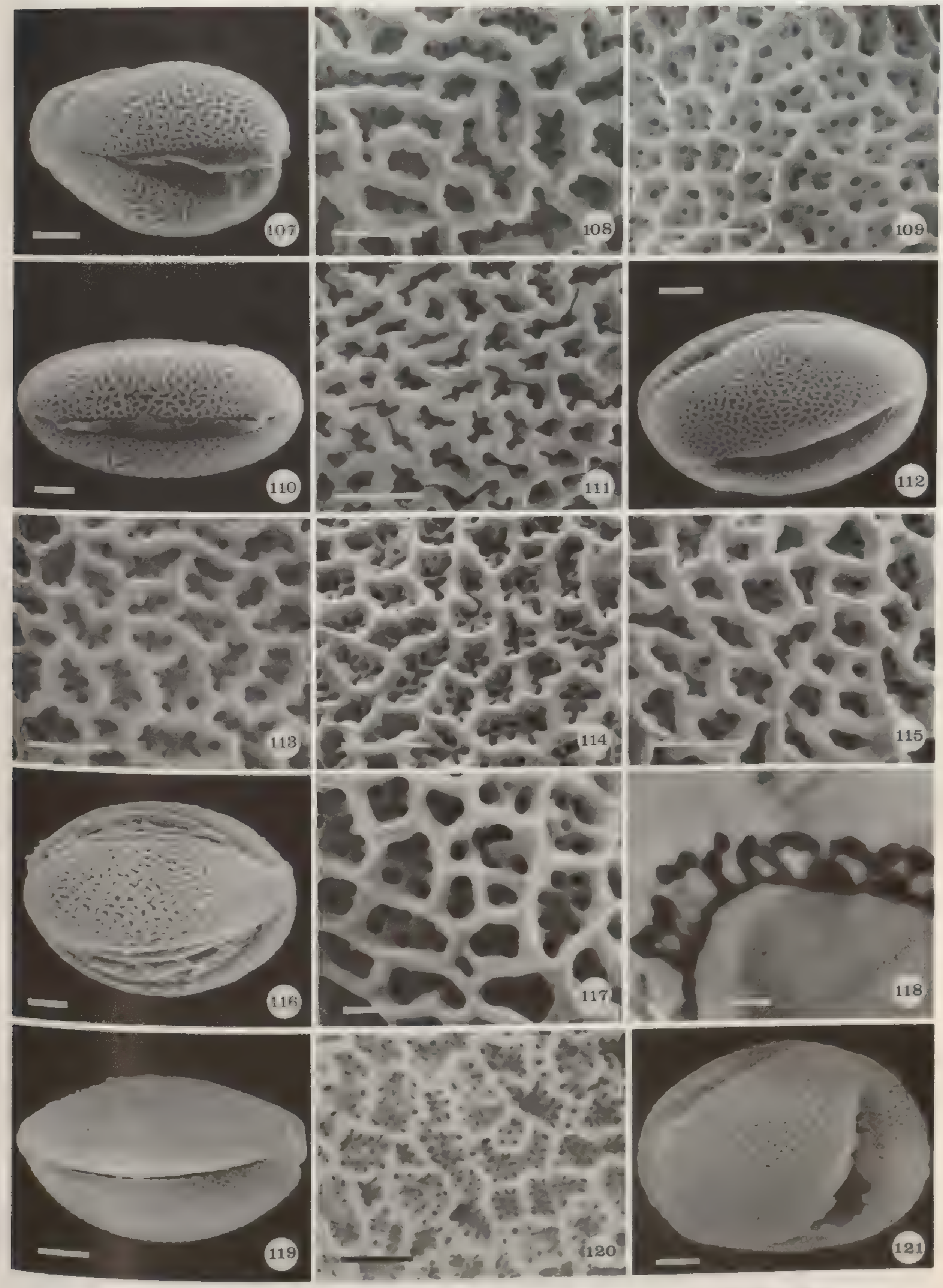




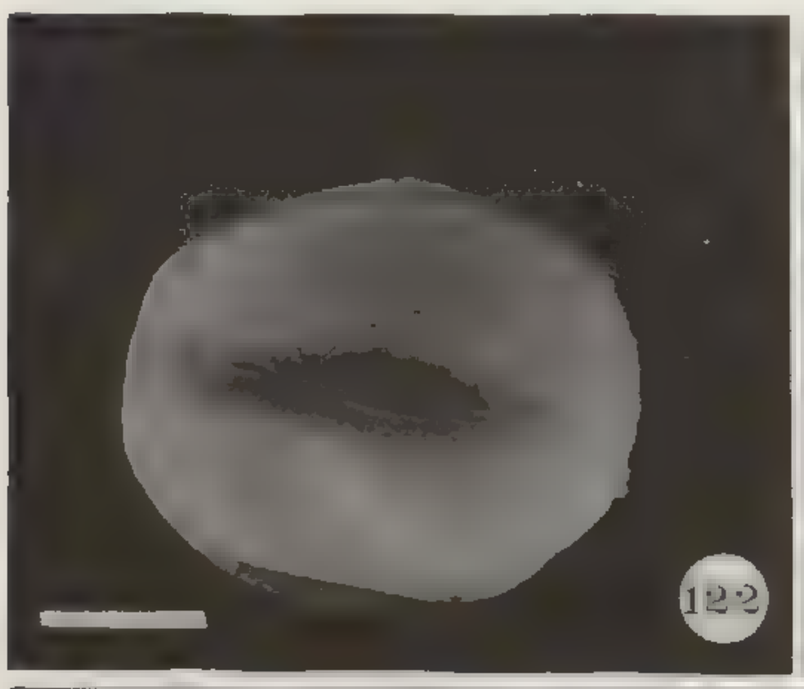


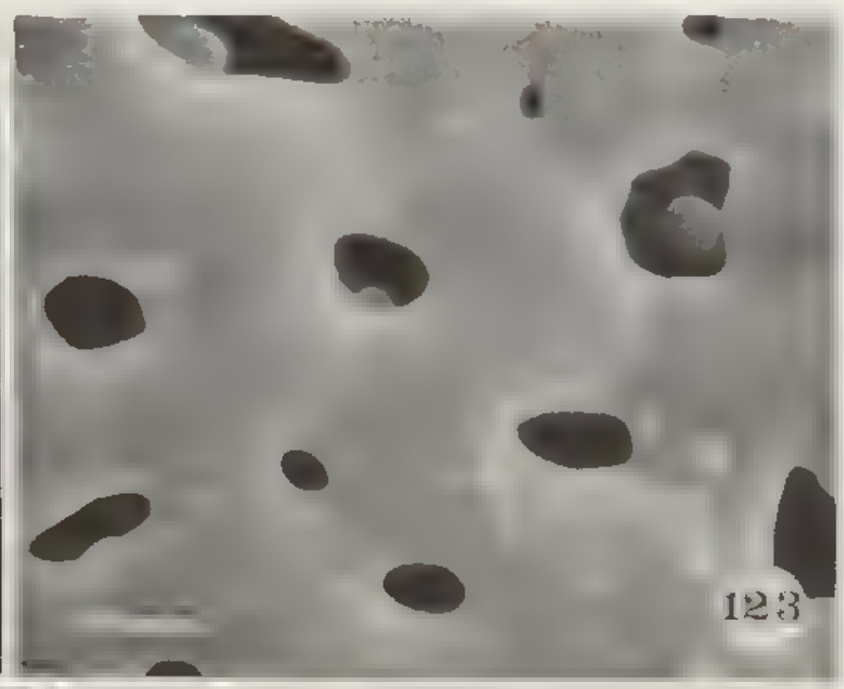
FIGURES 77–91. Pollen of Lamioideae: *Lagopsis*, *Lamiophlomis*, and *Lamium*. —77. *Lagopsis marrubiastrum*. —78, 79. *Lamiophlomis rotata*. —80, 81. *Lamium album*. —82, 83. *Lamium flexuosum*. —84, 85. *Lamium garganicum*. 86, 87. *Lamium galeobdolon*. —88, 89. *Lamium moschatum*. —90, 91. *Lamium purpureum*. Scales = 0.5 μm (83, 89); 1 μm (79, 81, 82, 84, 85, 87, 91); 5 μm (77, 78, 80, 86, 88, 90).

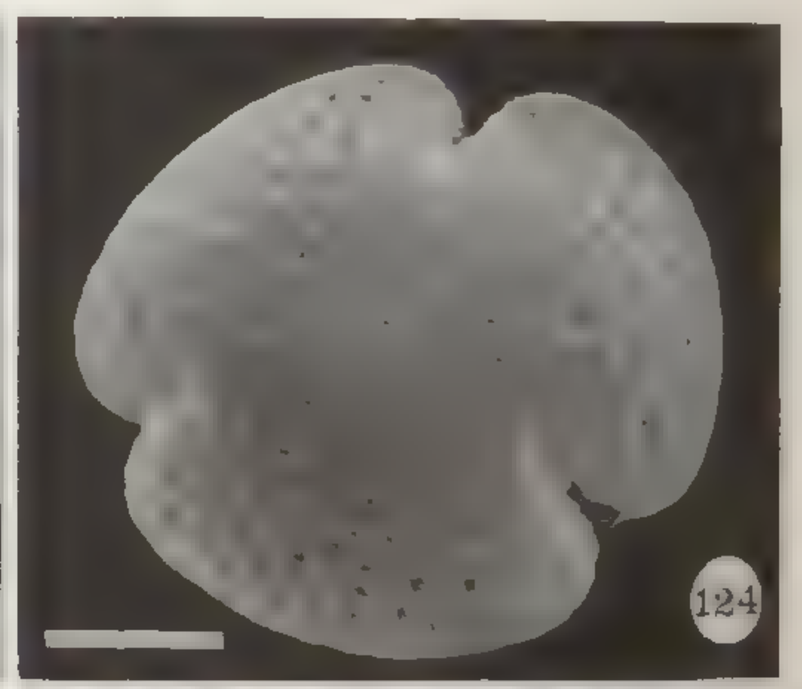
FIGURES 92–106. Pollen of Lamioideae: *Leonotis*, *Leonurus*, *Loxocalyx*, and *Macbridea*. —92, 93. *Leonotis bequaertii*. —94–96. *Leonotis leonitis*. —97. *Leonotis mollissima*. —98, 99. *Leonurus cardiaca* (*Swanson 811*). —100. *Leonurus sibiricus*. —101. *Loxocalyx ambiguus*. —102, 103. *Loxocalyx urticifolius*. —104. *Macbridea alba* (*Anonymous 4199*). —105, 106. *Macbridea caroliniana*. Scales = 1 μm (93, 95, 96, 97, 99, 100, 101, 103, 104, 106); 2.5 μm (98, 102); 5 μm (92, 94, 105).

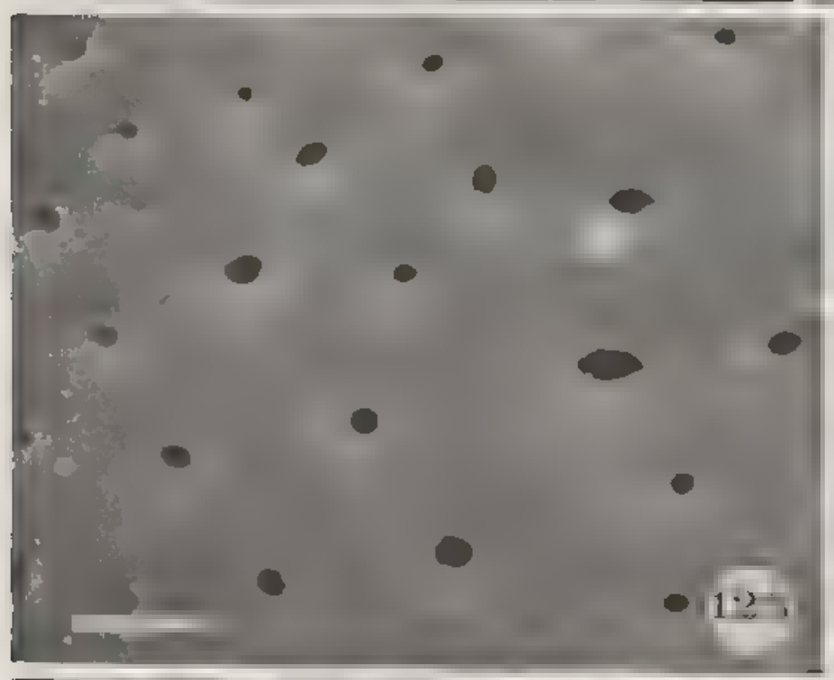


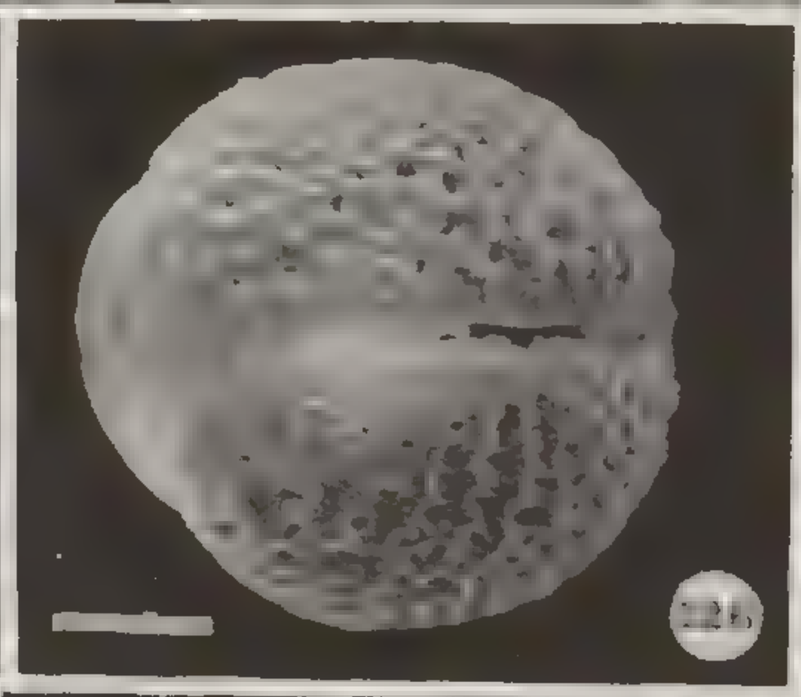
FIGURES 107–121. Pollen of Lamioideae: *Leucas*, *Melittis*, and *Metastachydium*. —107, 108. *Leucas abyssinica*. —109. *Leucas alluaudii*. —110, 111. *Leucas aspera*. —112, 113. *Leucas calostachys*. —114. *Leucas eriostoma*. —115. *Leucas hirta*. —116. *Leucas inflata*. —117. *Leucas javanica*. —118. *Leucas rosmarinifolia*. —119, 120. *Melittis melissophyllum*. —121. *Metastachydium sagittatum*. Scales = 0.5 μm (117, 118); 1 μm (108, 109, 111, 113, 114, 115, 120); 2.5 μm (107, 110, 112, 116, 121); 5 μm (119).

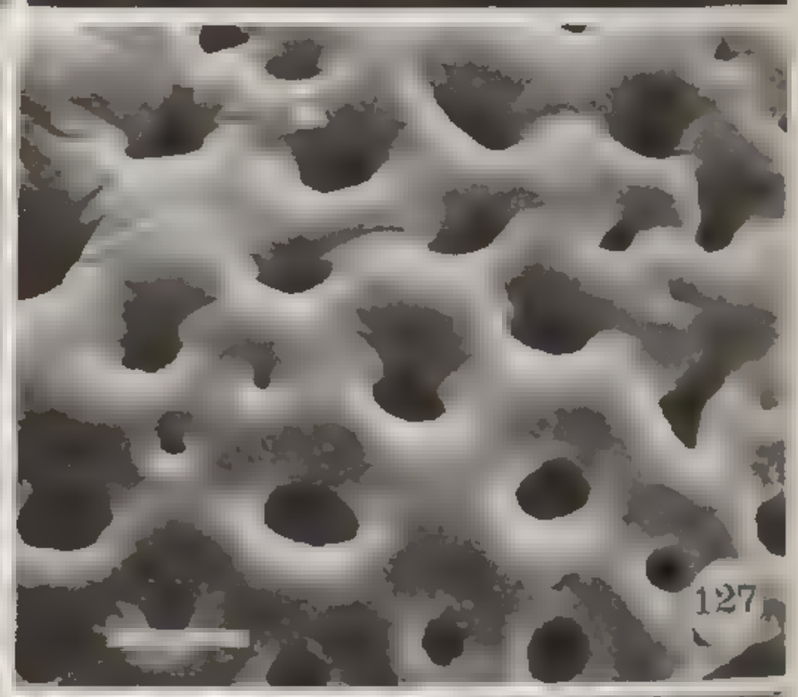


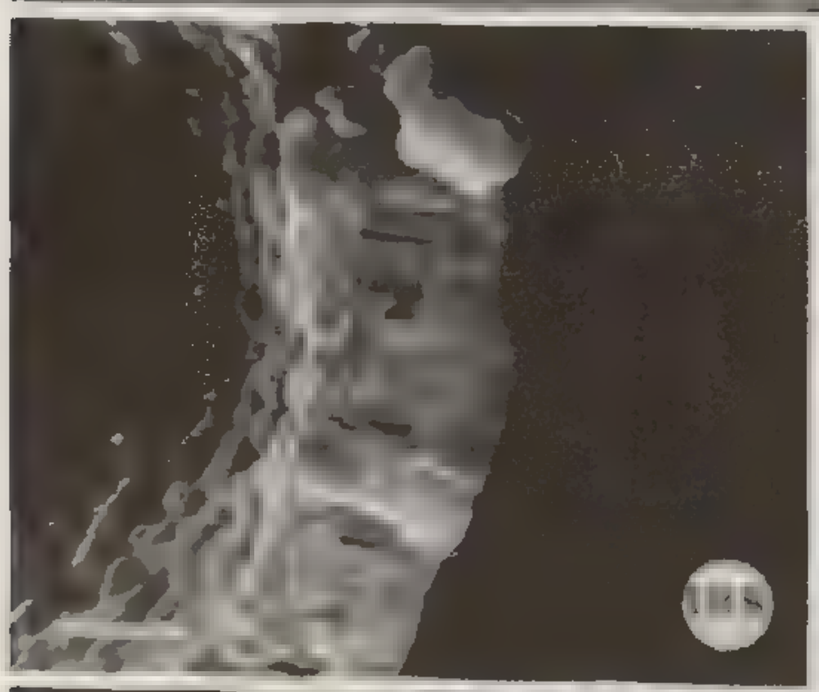


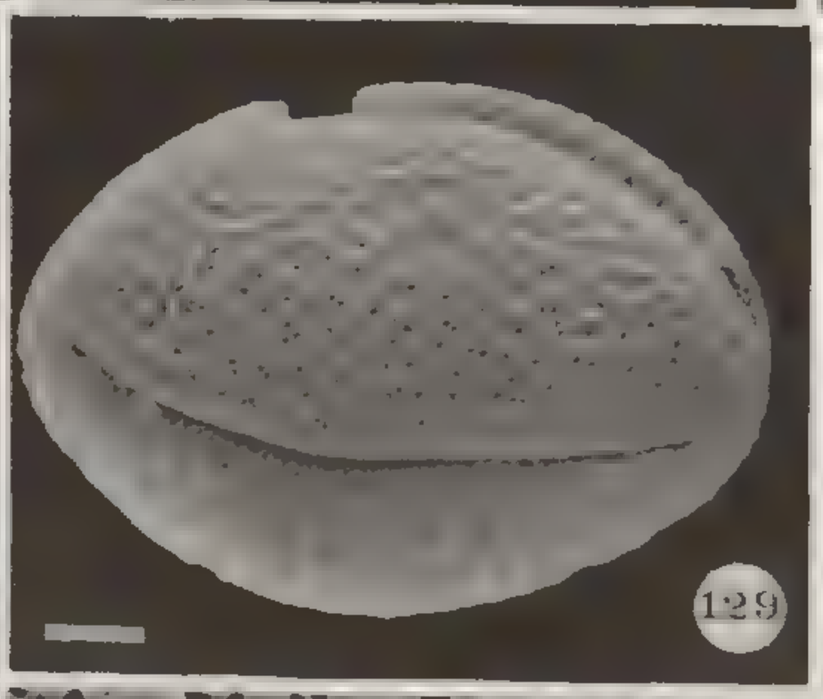


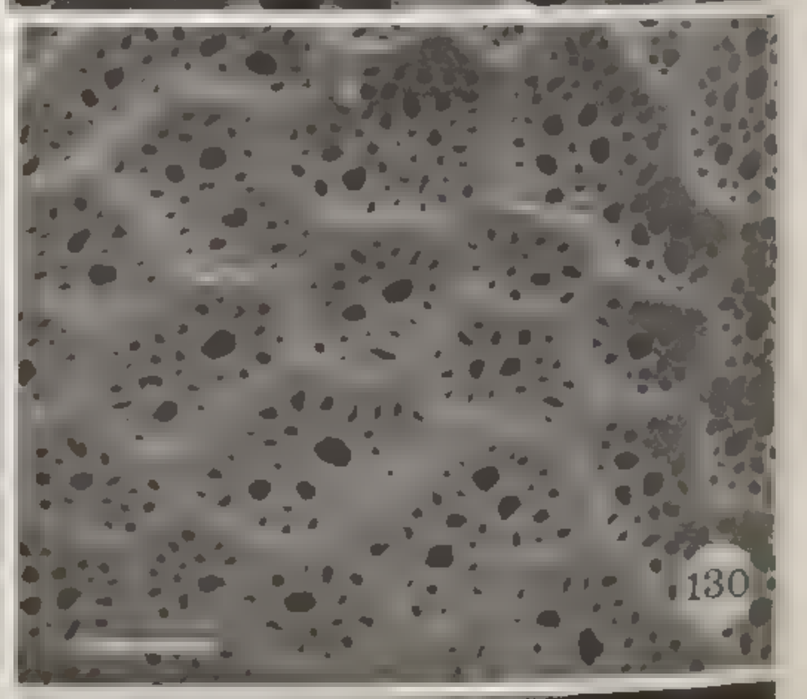


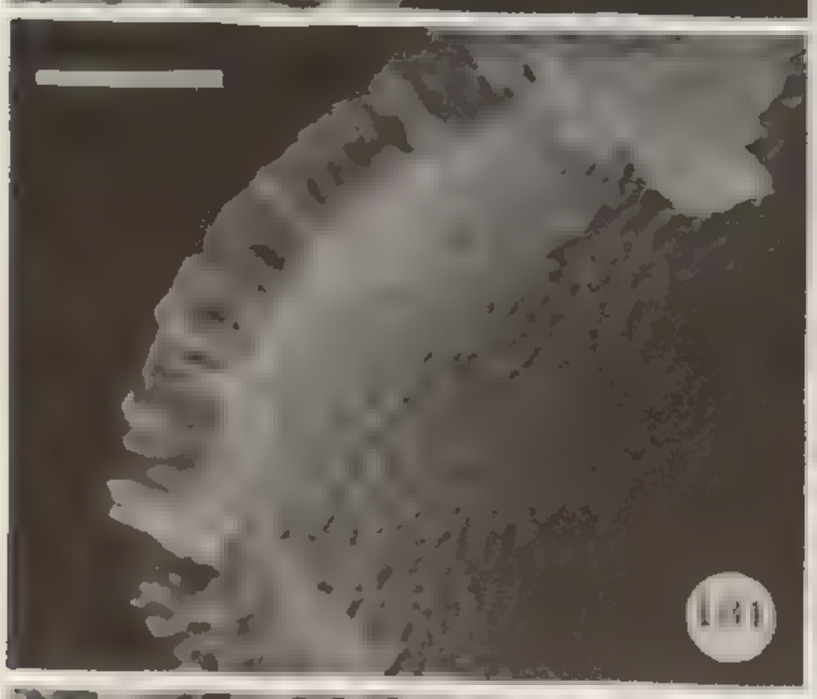


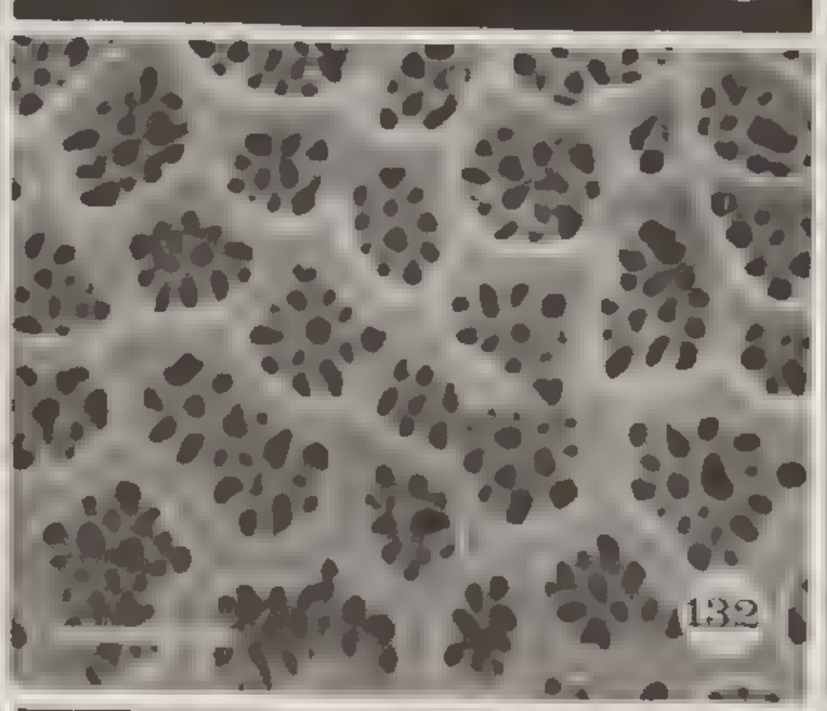


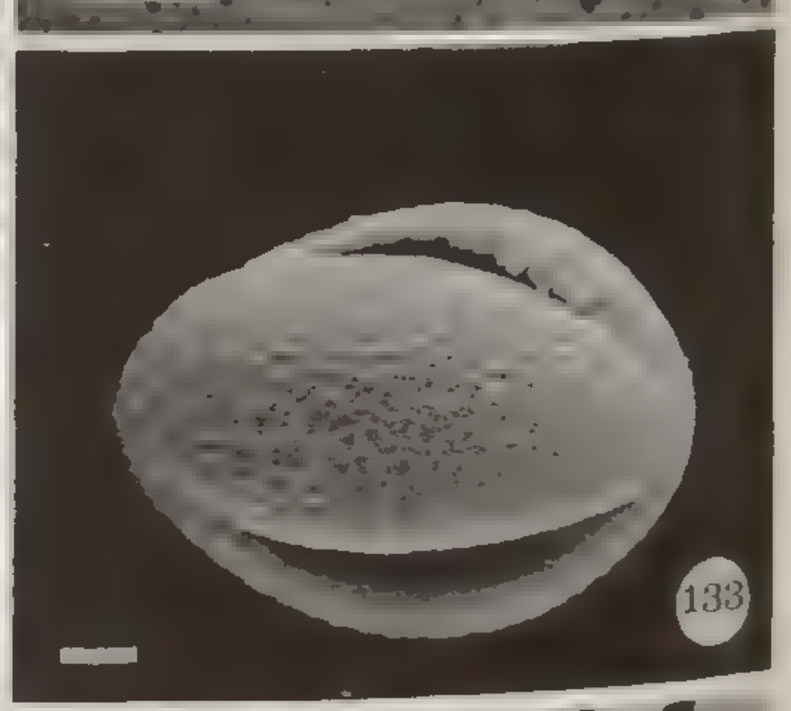


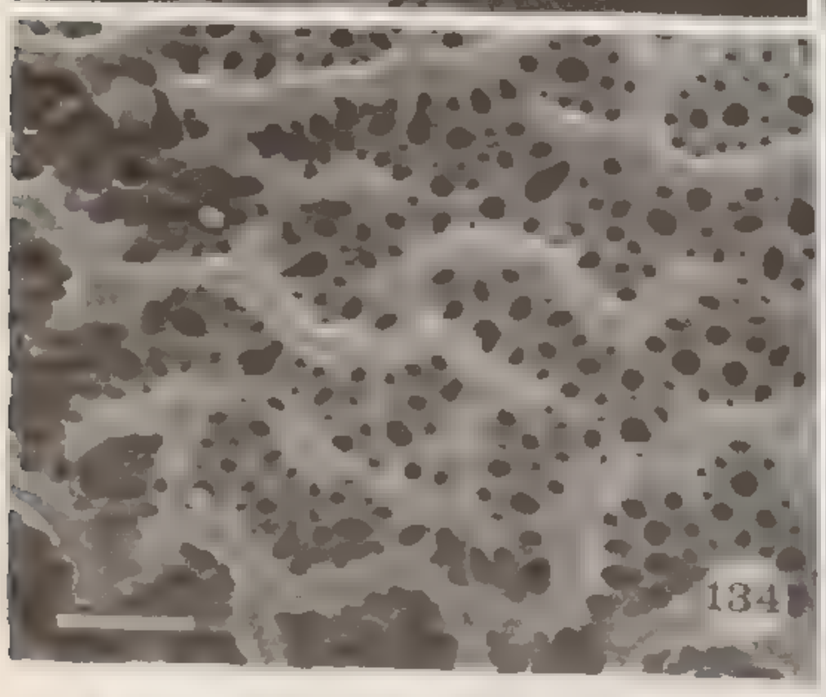


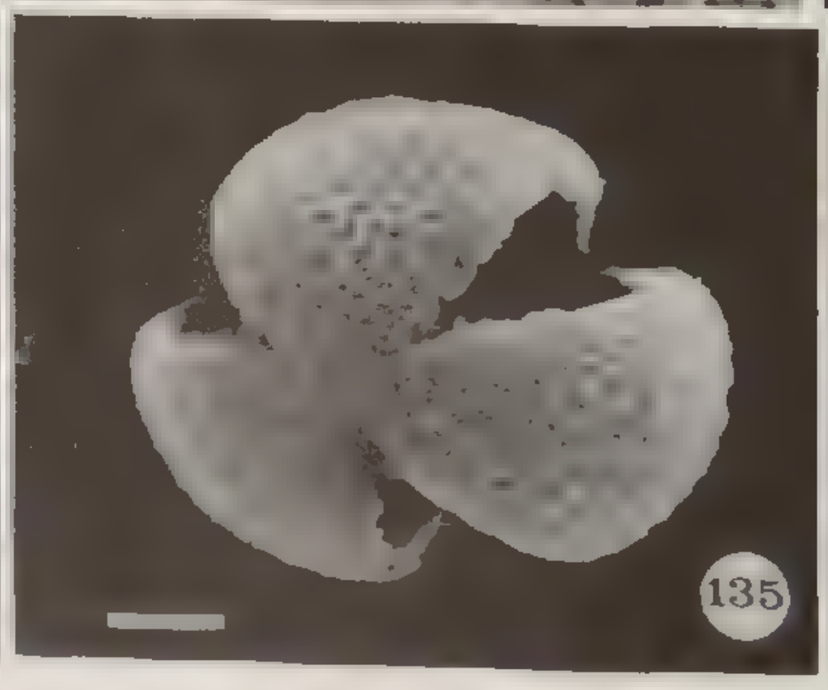


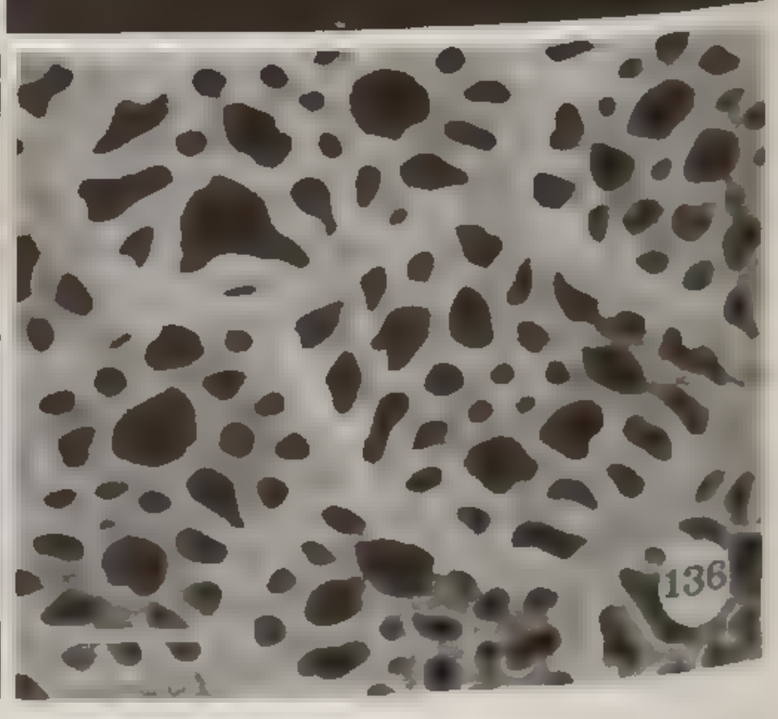






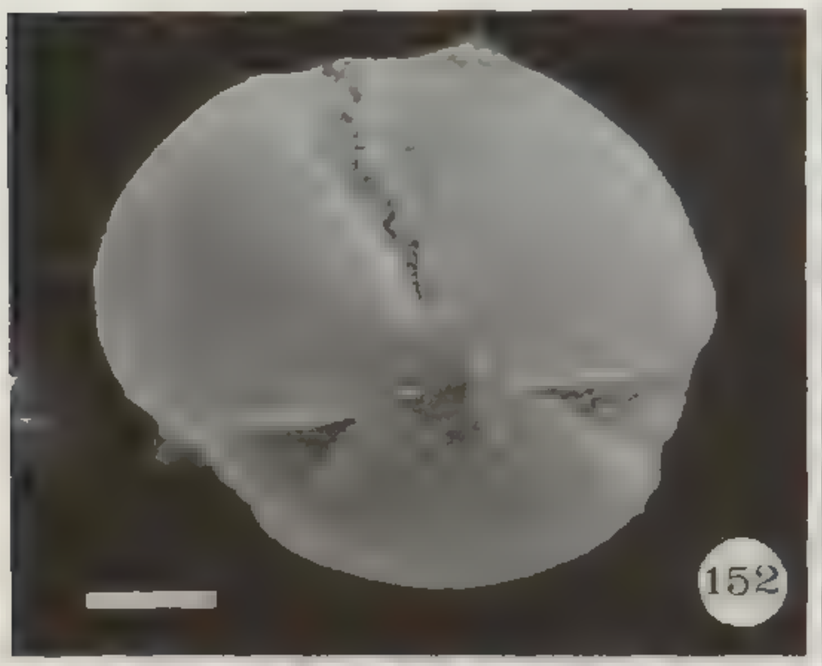


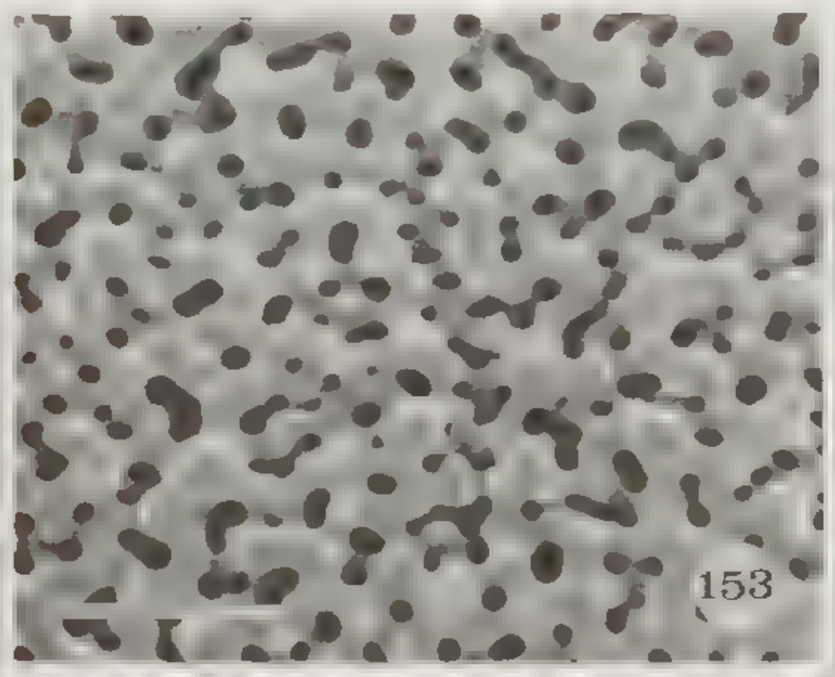


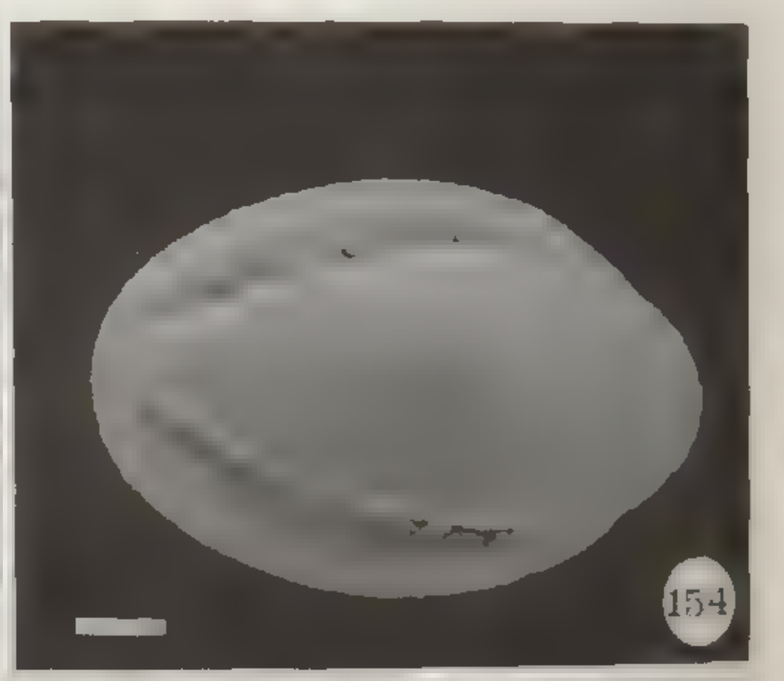


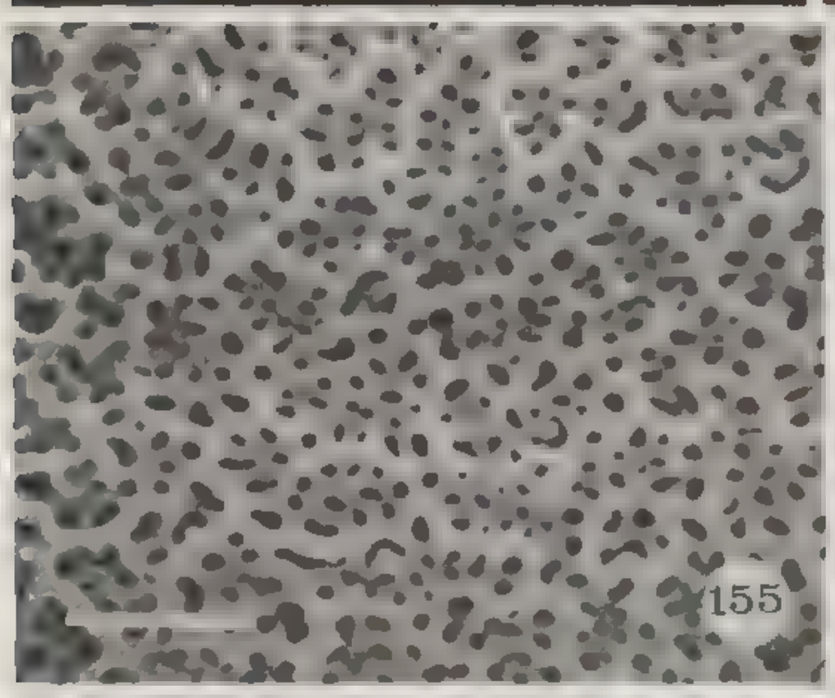
FIGURES 122–136. Pollen of Lamioideae: *Marrubium* and *Microtoena*. —122, 123. *Marrubium anisodon*. —124, 125. *Marrubium heterodon*. —126–128. *Marrubium supinum*. —129–131. *Microtoena delavayi*. —132. *Microtoena insuavis*. 133, 134. *Microtoena robusta*. —135, 136. *Microtoena urticifolia*. Scales = 0.5 μm (123); 1 μm (125, 127, 128, 130, 131, 132, 134, 136); 2.5 μm (129, 133); 5 μm (122, 124, 126, 135).

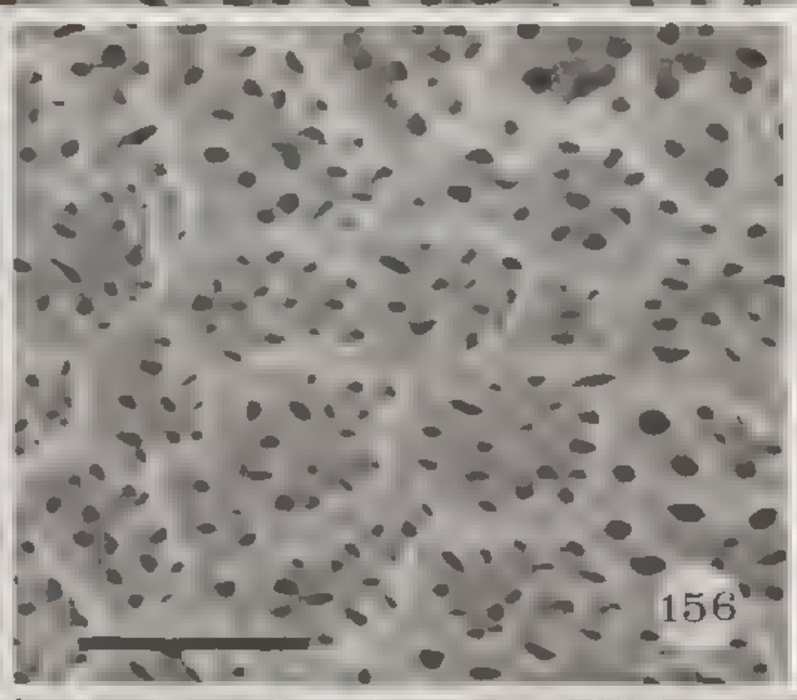
FIGURES 137–151. Pollen of Lamioideae: *Moluccella*, *Notochaete*, *Otostegia*, *Panzerina*, and *Paralamium*. —137. *Moluccella laevis*. —138, 139. *Moluccella spinosa*. —140, 141. *Notochaete hamosa*. —142, 143. *Otostegia fruticosa*. 144. *Otostegia integrifolia*. —145. *Otostegia repanda*. 146, 147. *Otostegia tomentosa*. —148, 149. *Panzerina lanata* (*Reverdatto 3775b*). —150. *Panzerina lanata* (*Steinberg & Prochorova 3459*). 151. *Paralamium gracile*. Scales = 0.5 μm (147); 1 μm (137, 139, 141, 143, 144, 145, 146, 149, 150, 151); 2.5 μm (142, 148); 5 μm (138, 140).

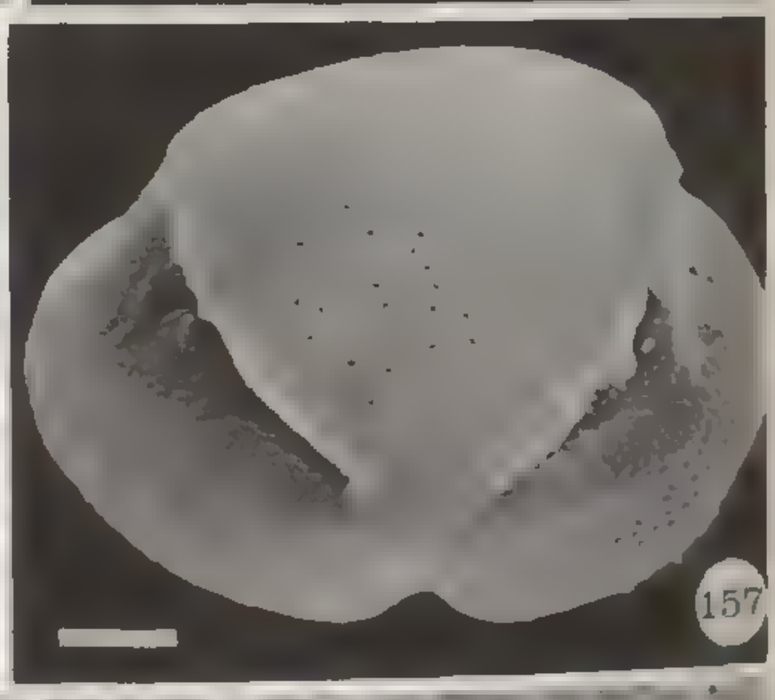


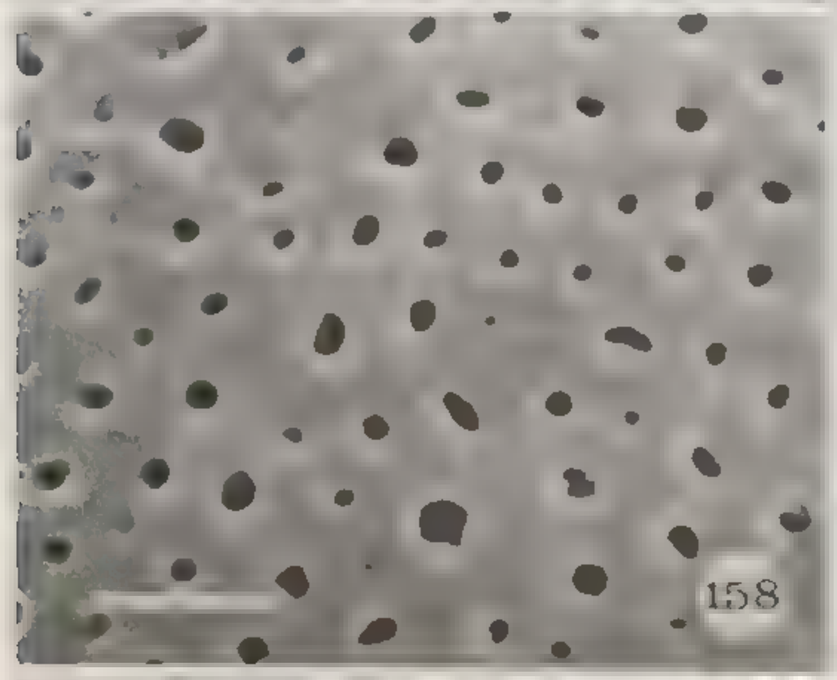


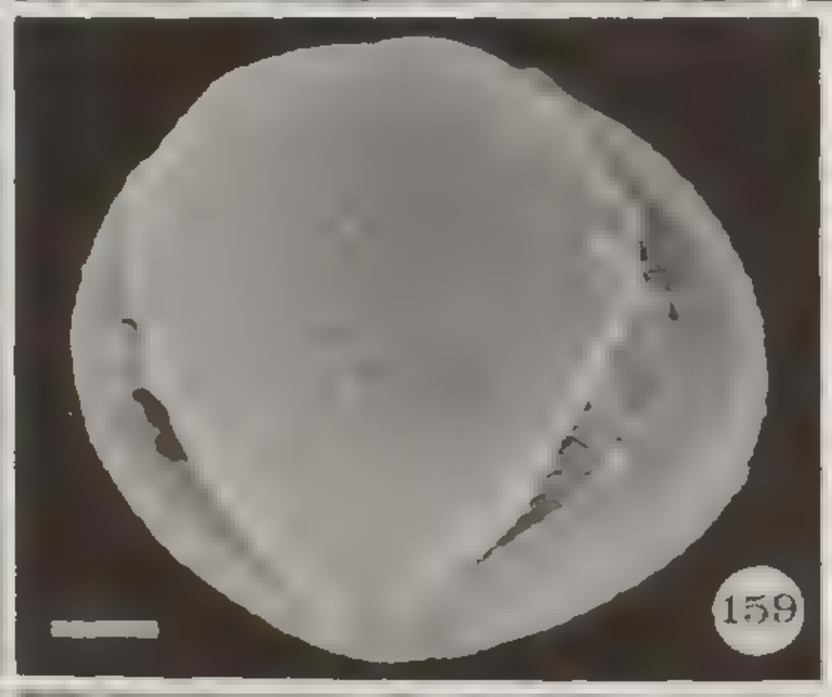


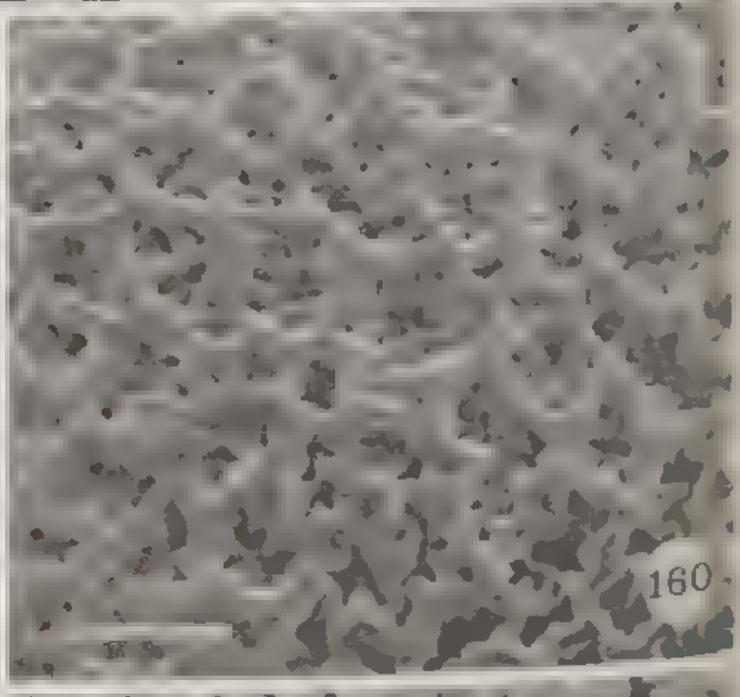


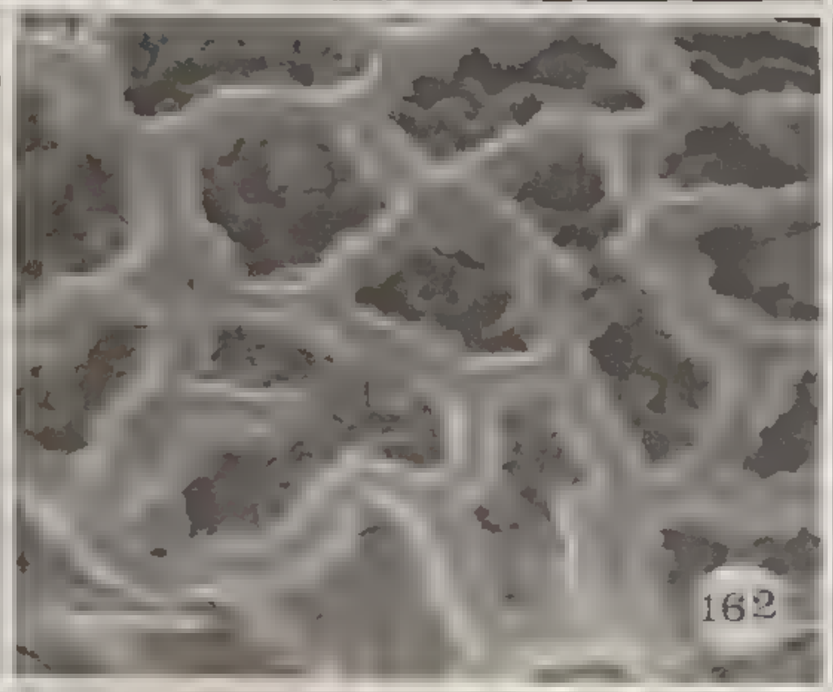


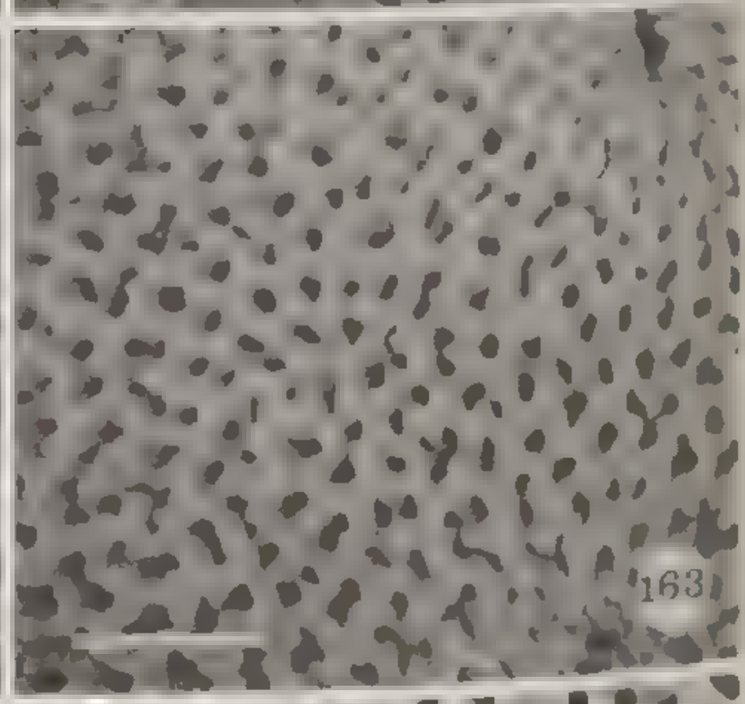


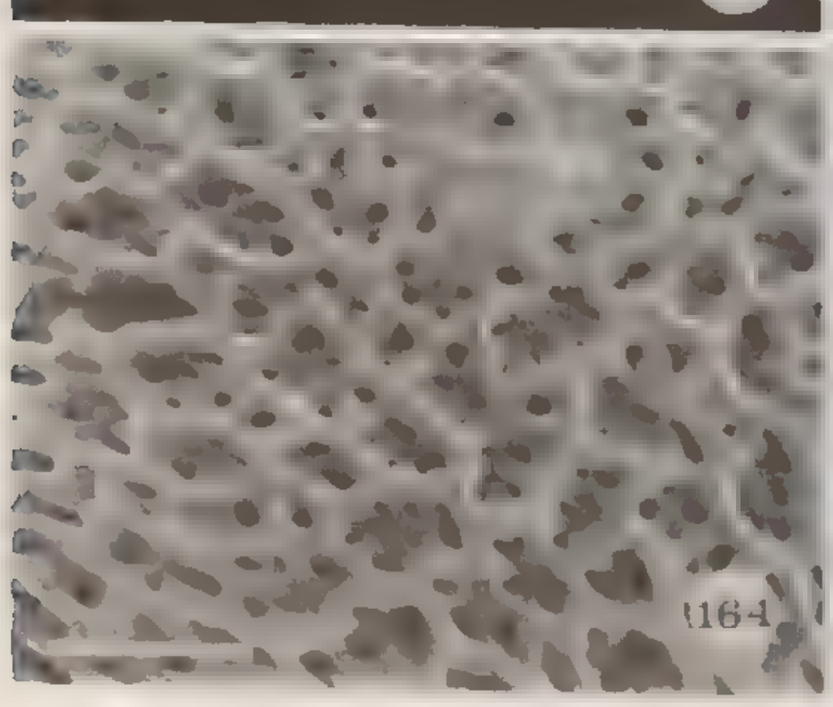


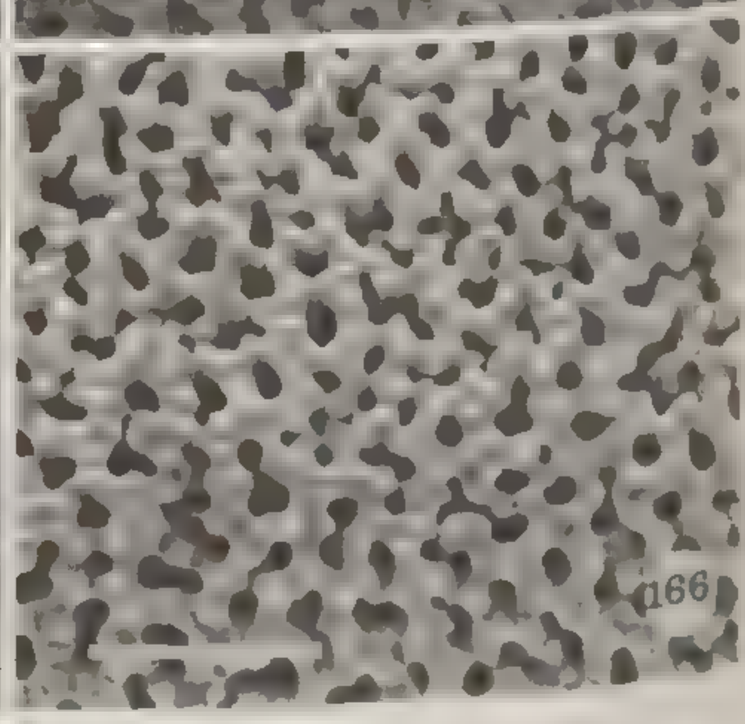




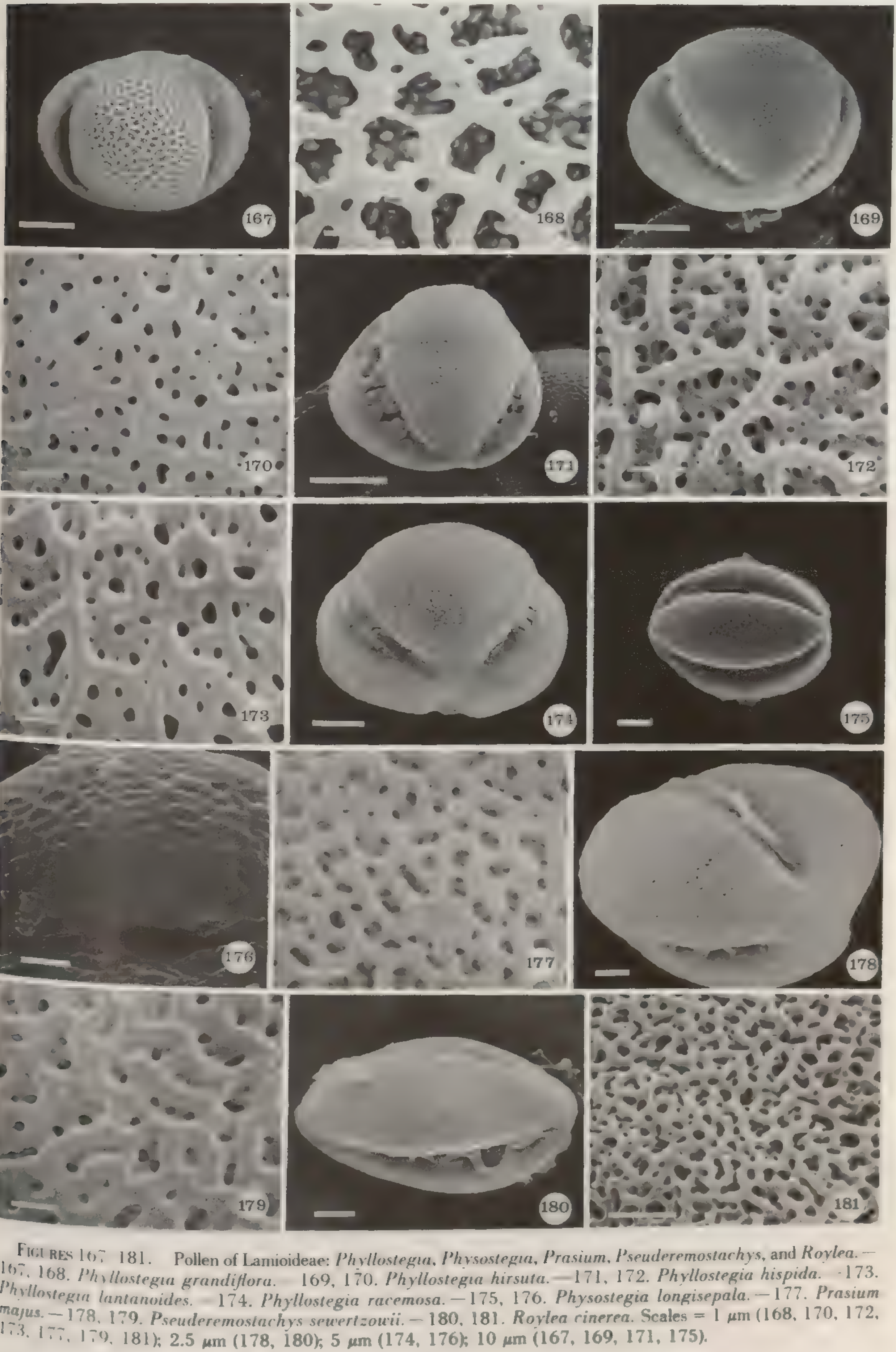




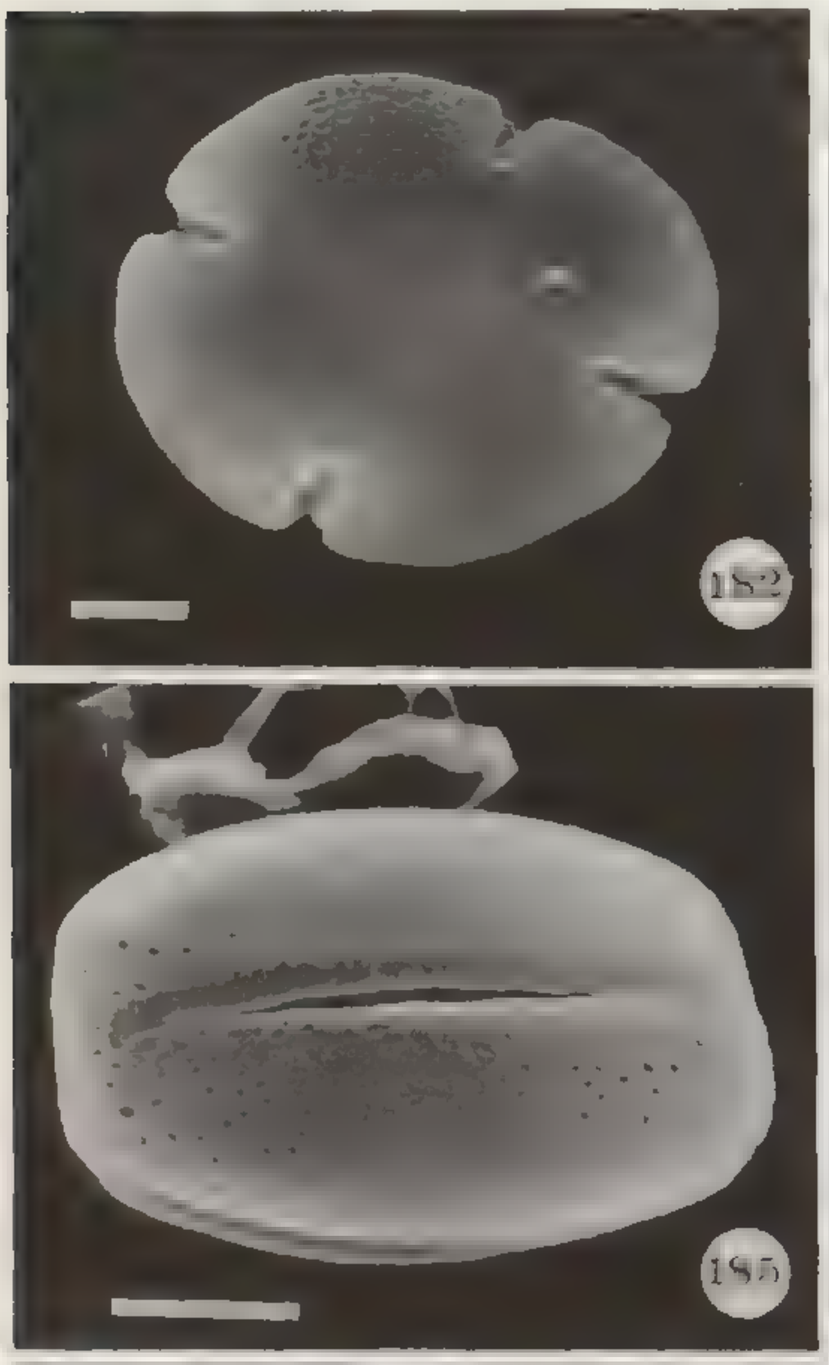


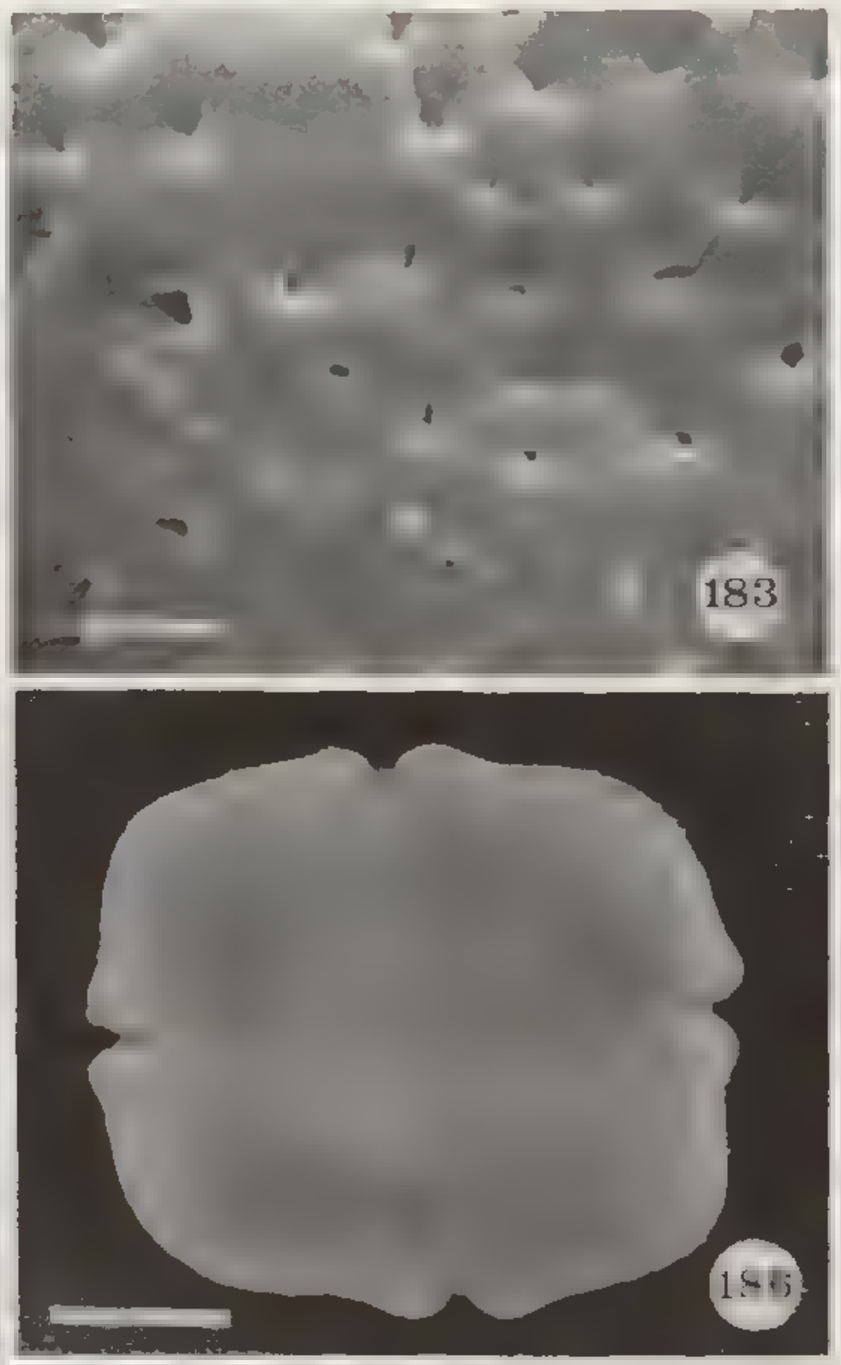


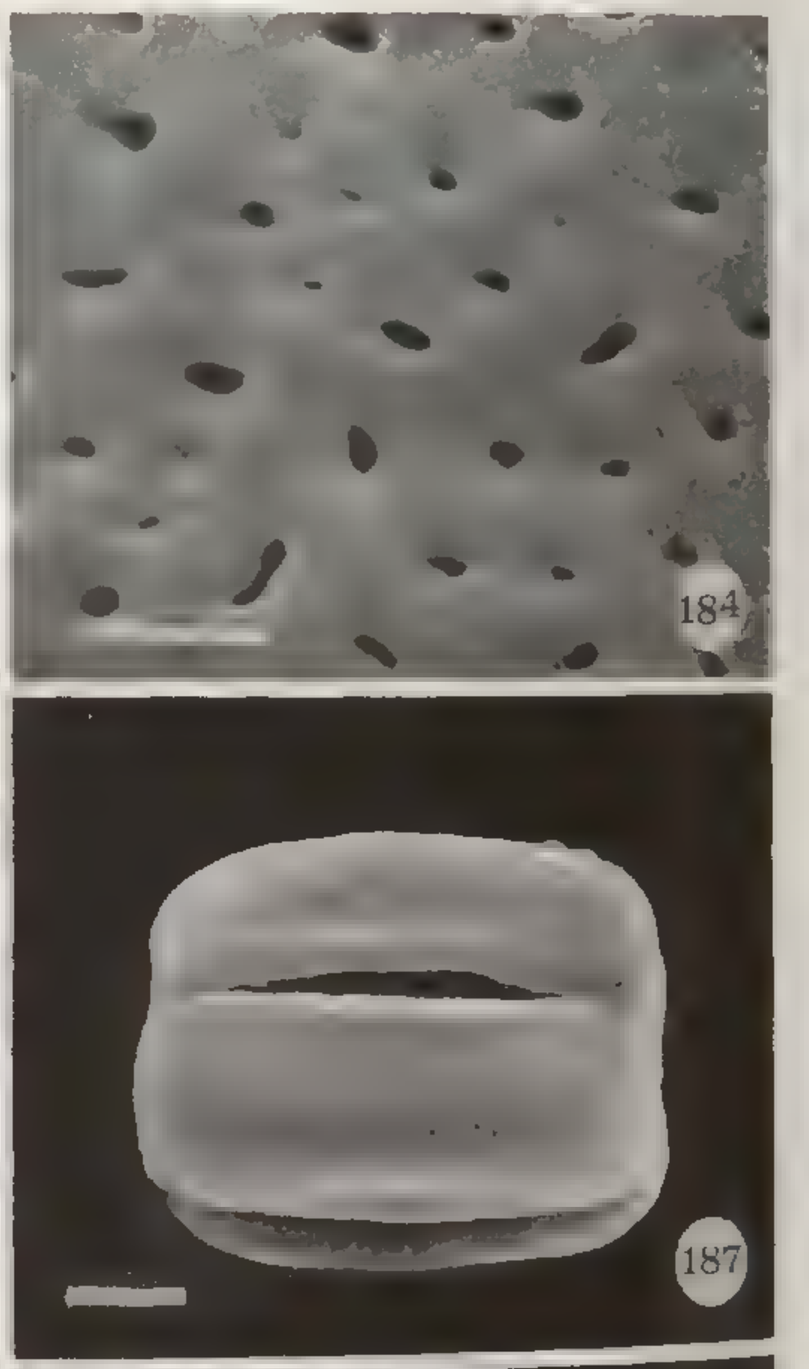
FIGURES 152–166. Pollen of Lamioideae: *Paraphlomis*, *Phlomidoschema*, and *Phlomis*.—152, 153. *Paraphlomis javanica*.—154, 155. *Paraphlomis lanceolata*.—156. *Paraphlomis rugosa*.—157, 158. *Phlomidoschema parviflorum*.—159, 160. *Phlomis agraria*.—161, 162. *Phlomis lanata*.—163. *Phlomis maximowiczii*.—164. *Phlomis tuberosa*.—165, 166. *Phlomis umbrosa*. Scales = 1 μm (153, 155, 156, 158, 160, 162, 163, 164, 166); 2.5 μm (154, 157, 159, 165); 5 μm (152, 161).

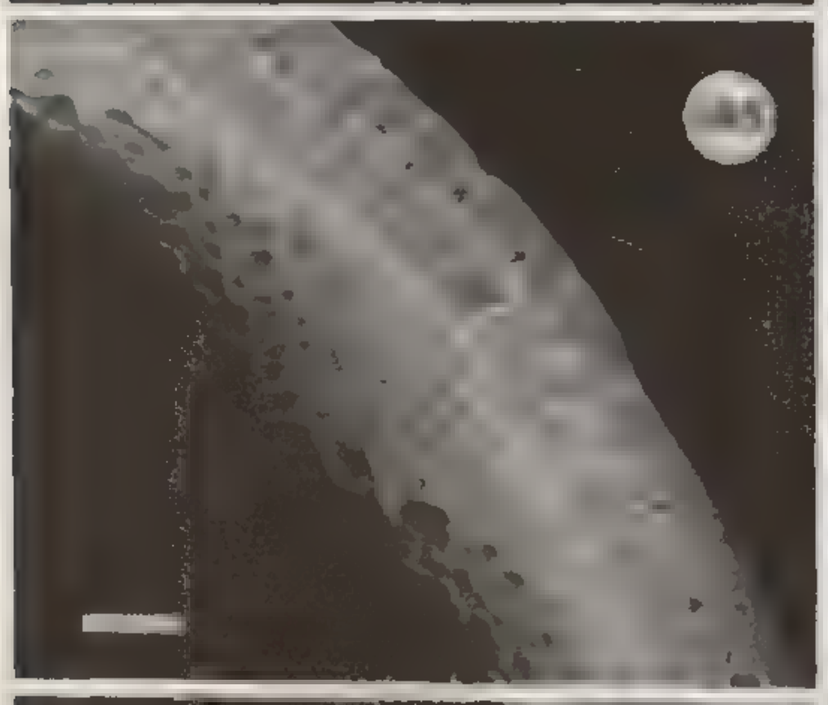


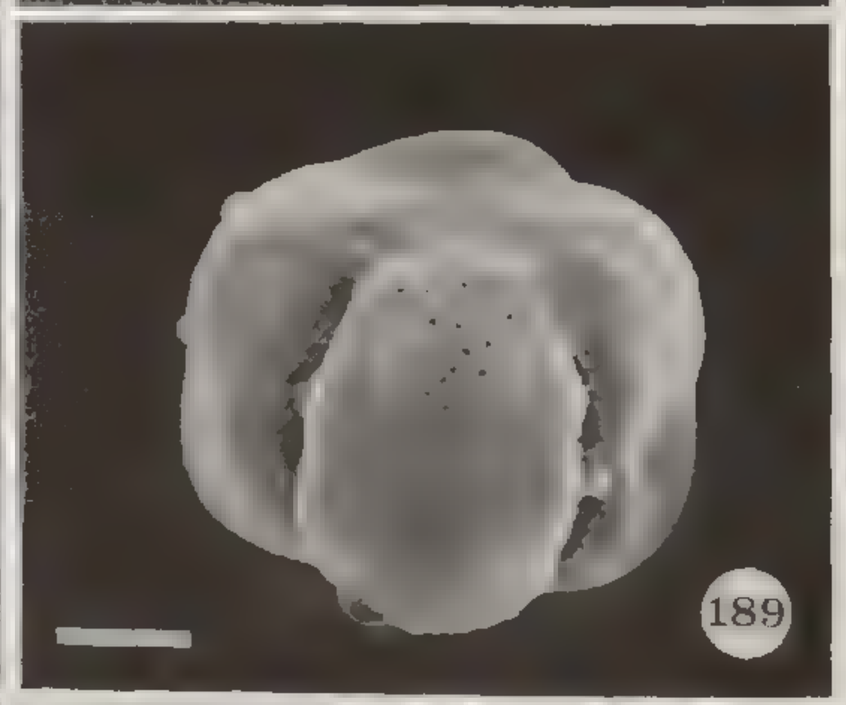
FIGURES 167–181. Pollen of Lamioideae: *Phyllostegia*, *Physostegia*, *Prasium*, *Pseuderemostachys*, and *Roylea*.—167, 168. *Phyllostegia grandiflora*.—169, 170. *Phyllostegia hirsuta*.—171, 172. *Phyllostegia hispida*.—173. *Phyllostegia lantanoides*.—174. *Phyllostegia racemosa*.—175, 176. *Physostegia longisepala*.—177. *Prasium majus*.—178, 179. *Pseuderemostachys sewertzowii*.—180, 181. *Roylea cinerea*. Scales = 1 μm (168, 170, 172, 173, 177, 179, 181); 2.5 μm (178, 180); 5 μm (174, 176); 10 μm (167, 169, 171, 175).

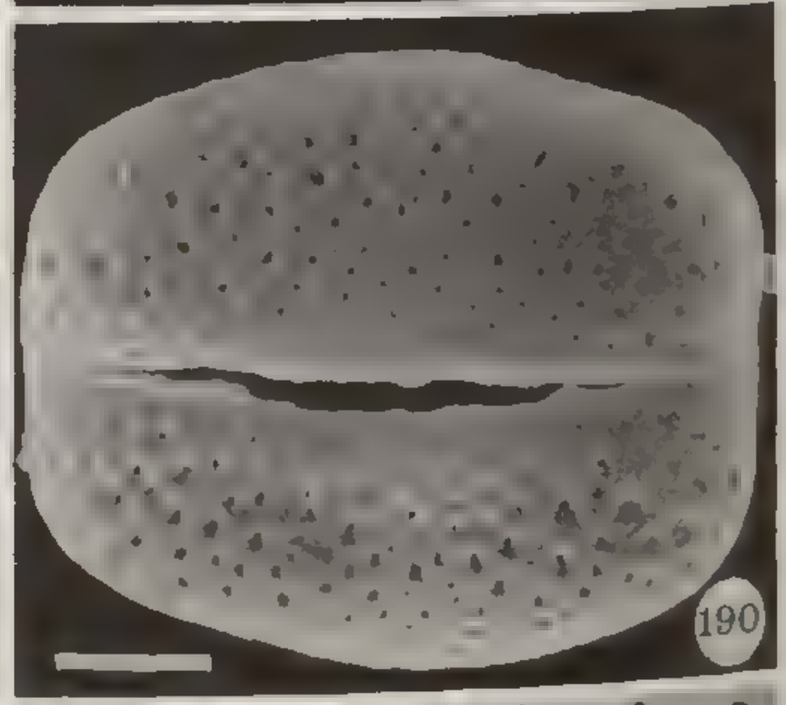


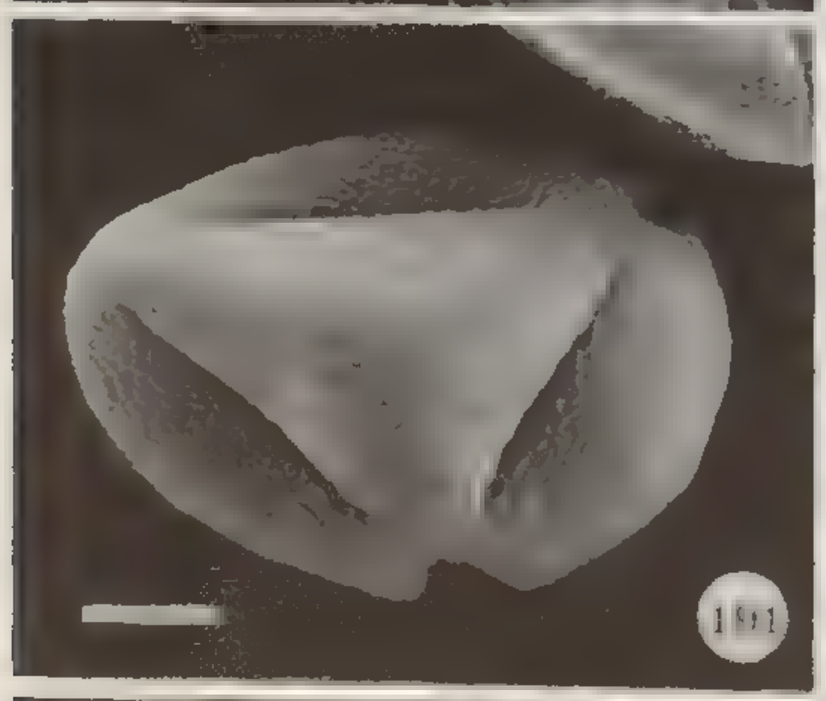


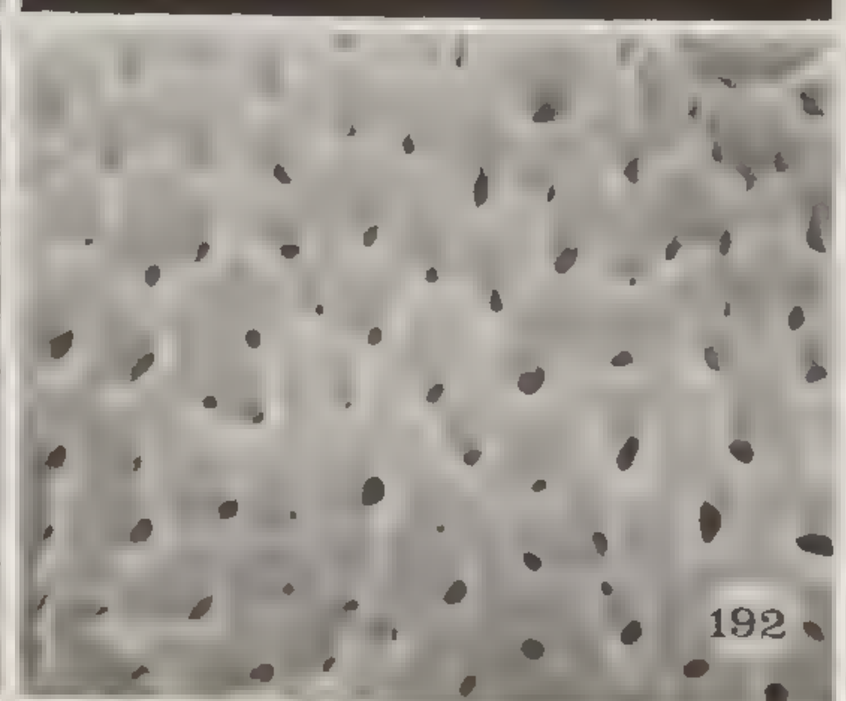


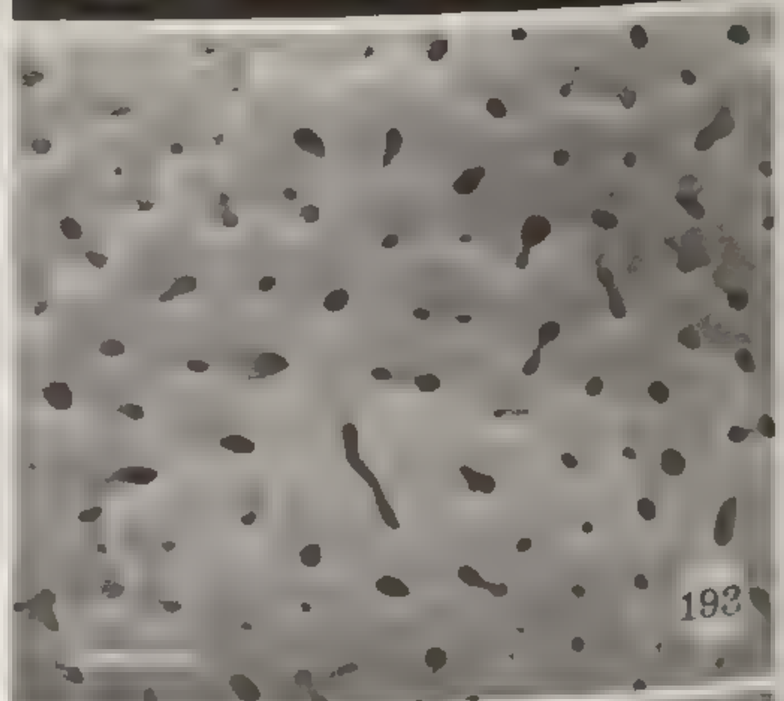


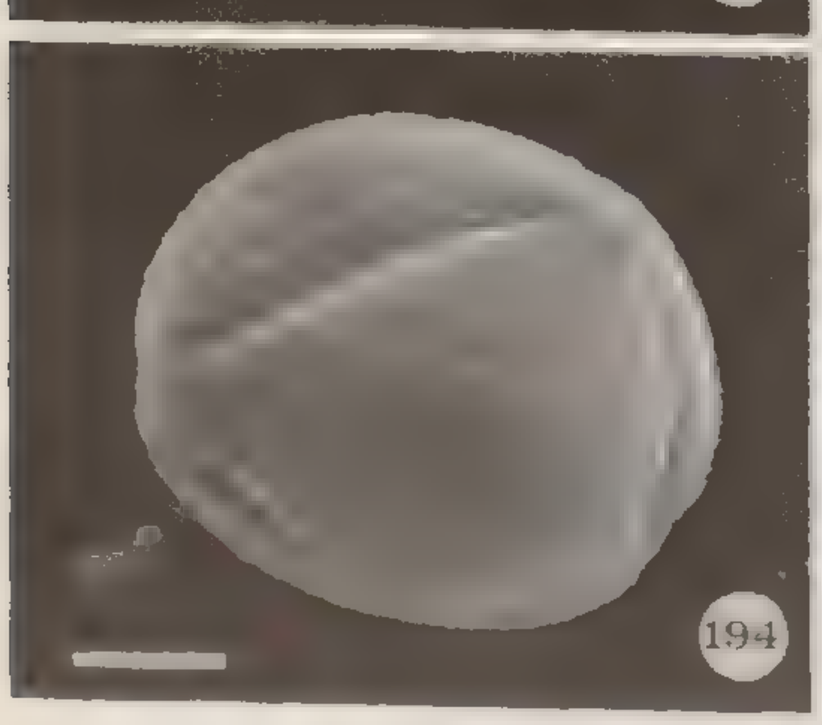


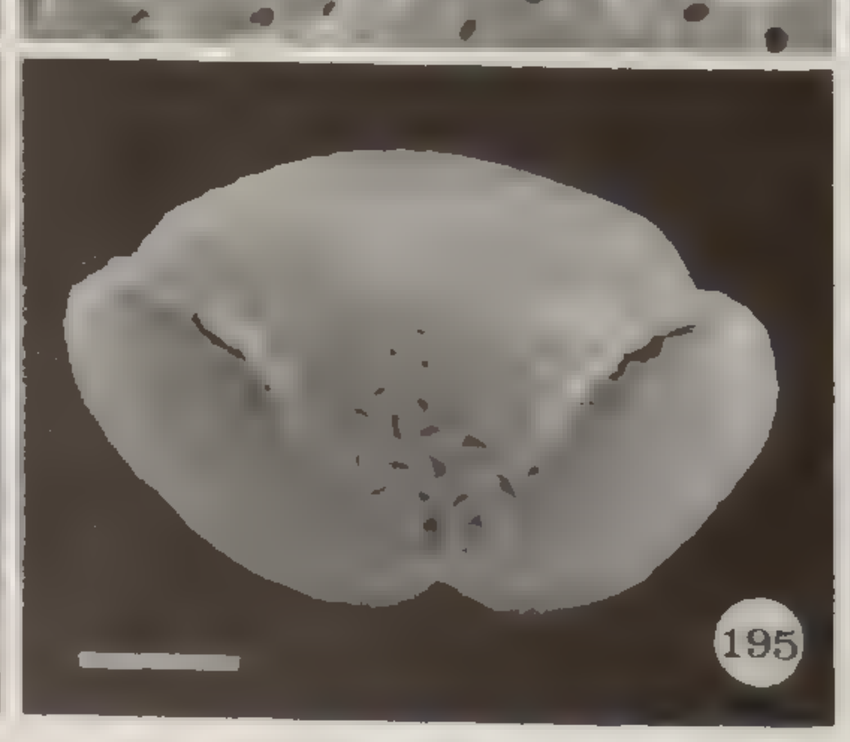


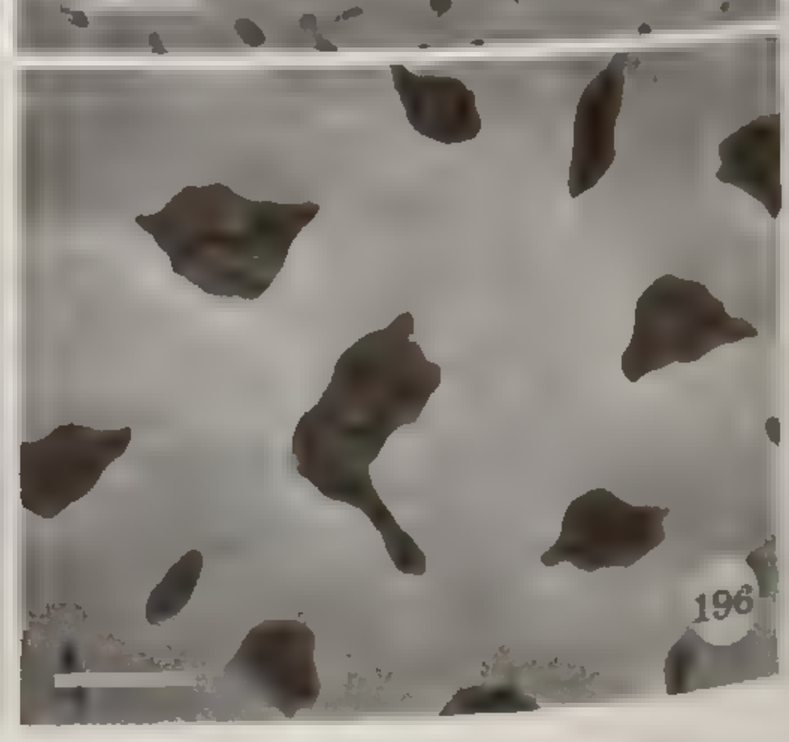




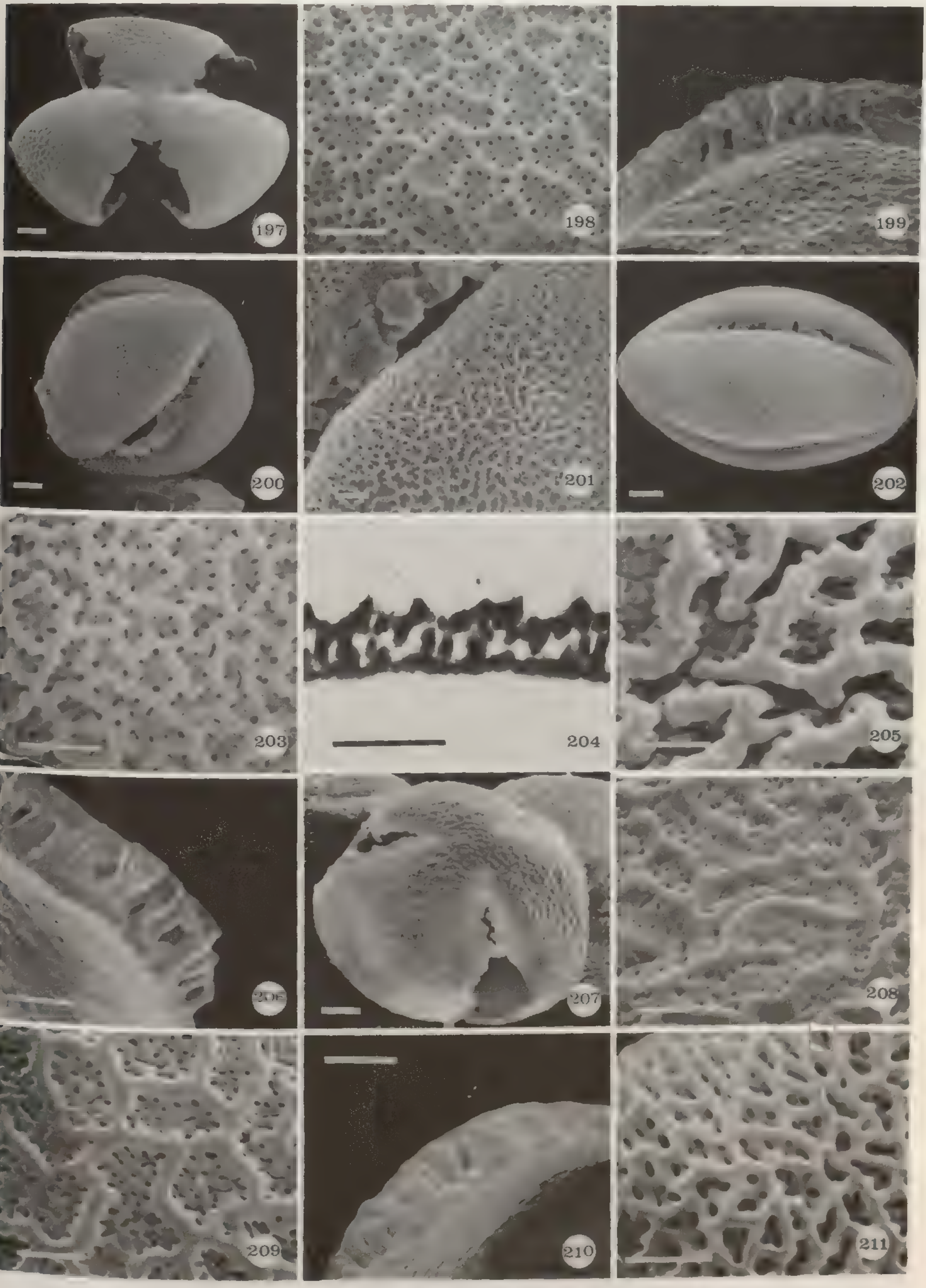






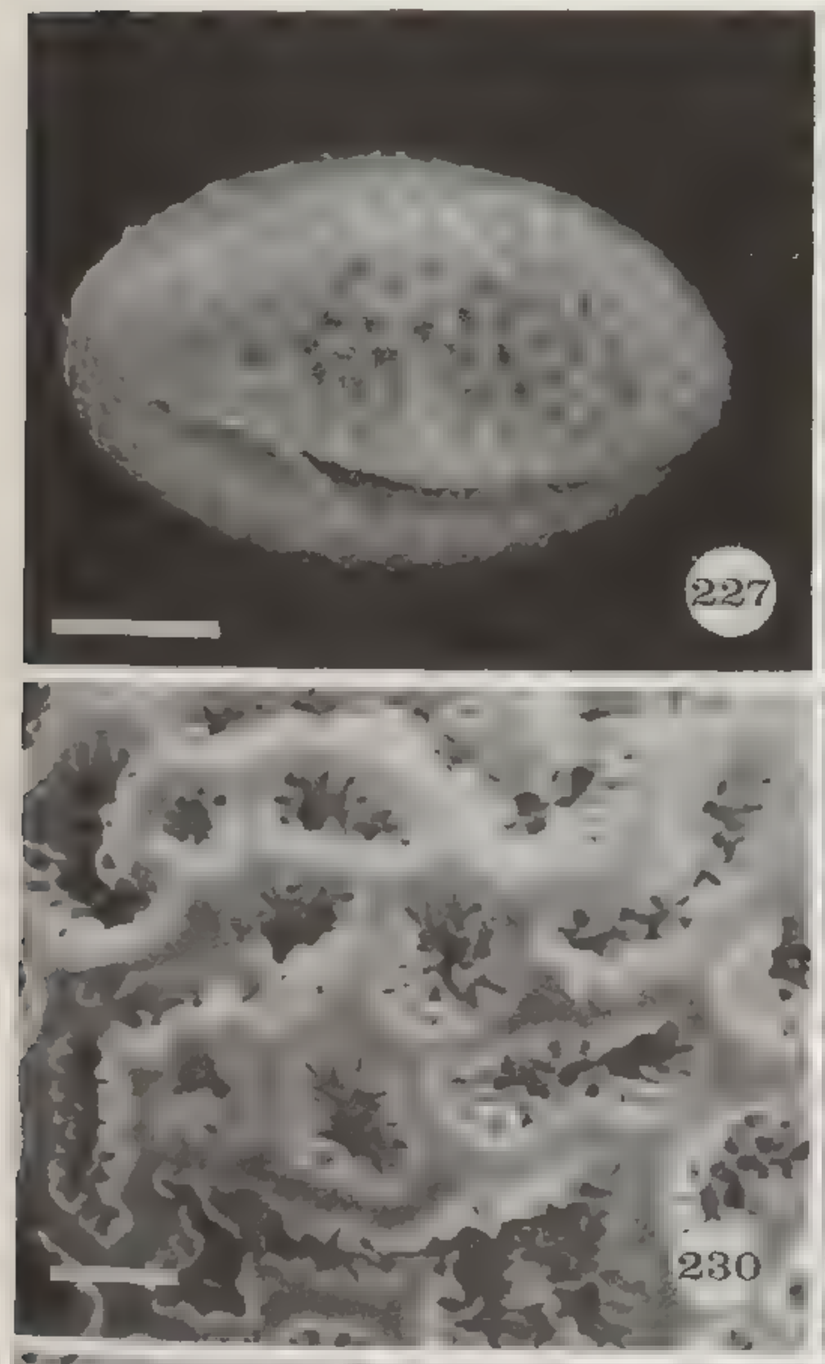


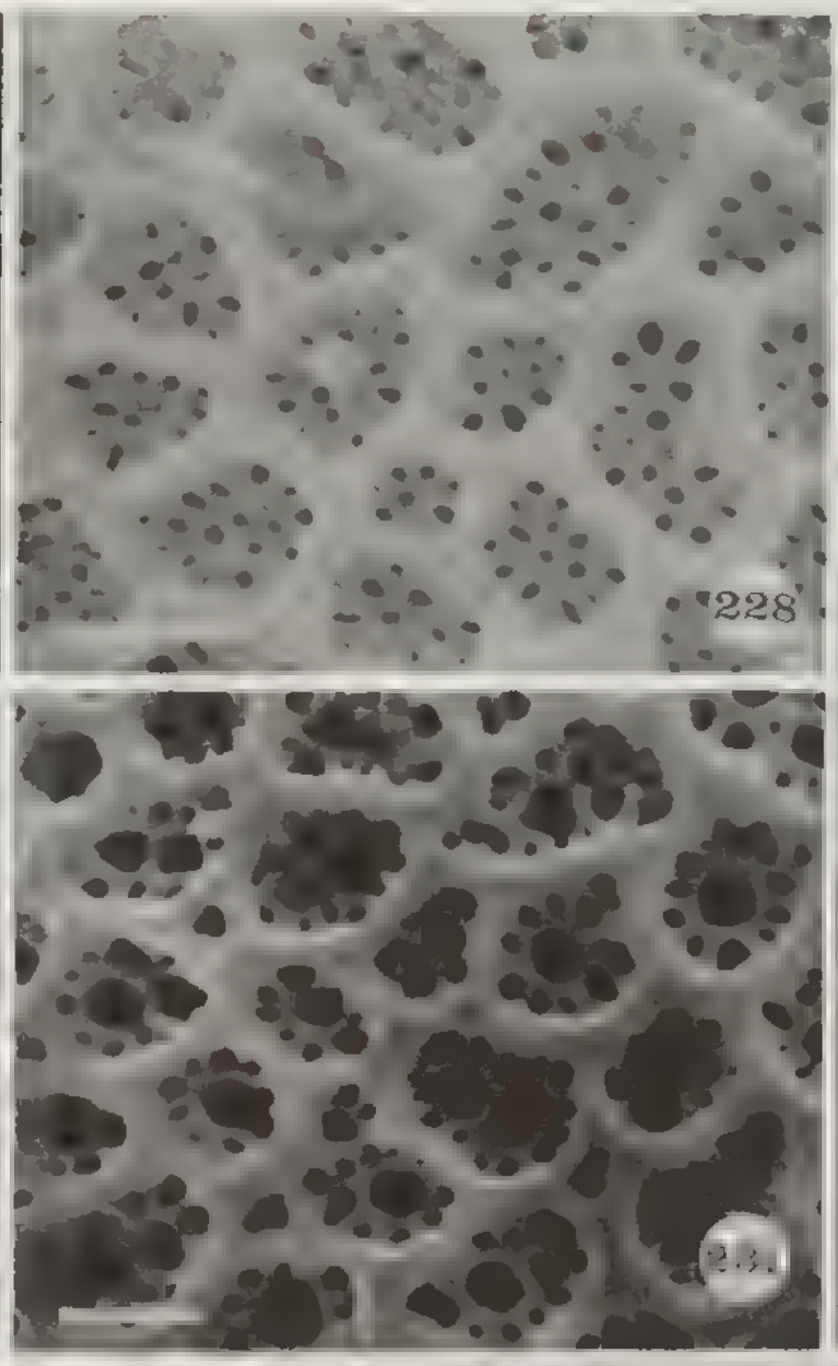
FIGURES 182–196. Pollen of Lamioideae: *Sideritis*. —182, 183. *Sideritis canariensis*. —184. *Sideritis candicans*. —185. *Sideritis curvidens*. —186. *Sideritis hyssopifolia*. —187. *Sideritis ilicifolia*. —188. *Sideritis lagascana*. —189. *Sideritis romana*. —190. *Sideritis villosa*. —191, 192. *Sideritis chlorostegia*. —193. *Sideritis cuboea*. —194. *Sideritis hololeuca*. —195, 196. *Sideritis montana*. Scales = 1 μm (183, 184, 188, 192, 193, 196); 5 μm (182, 185, 186, 187, 189, 190, 191, 194, 195).

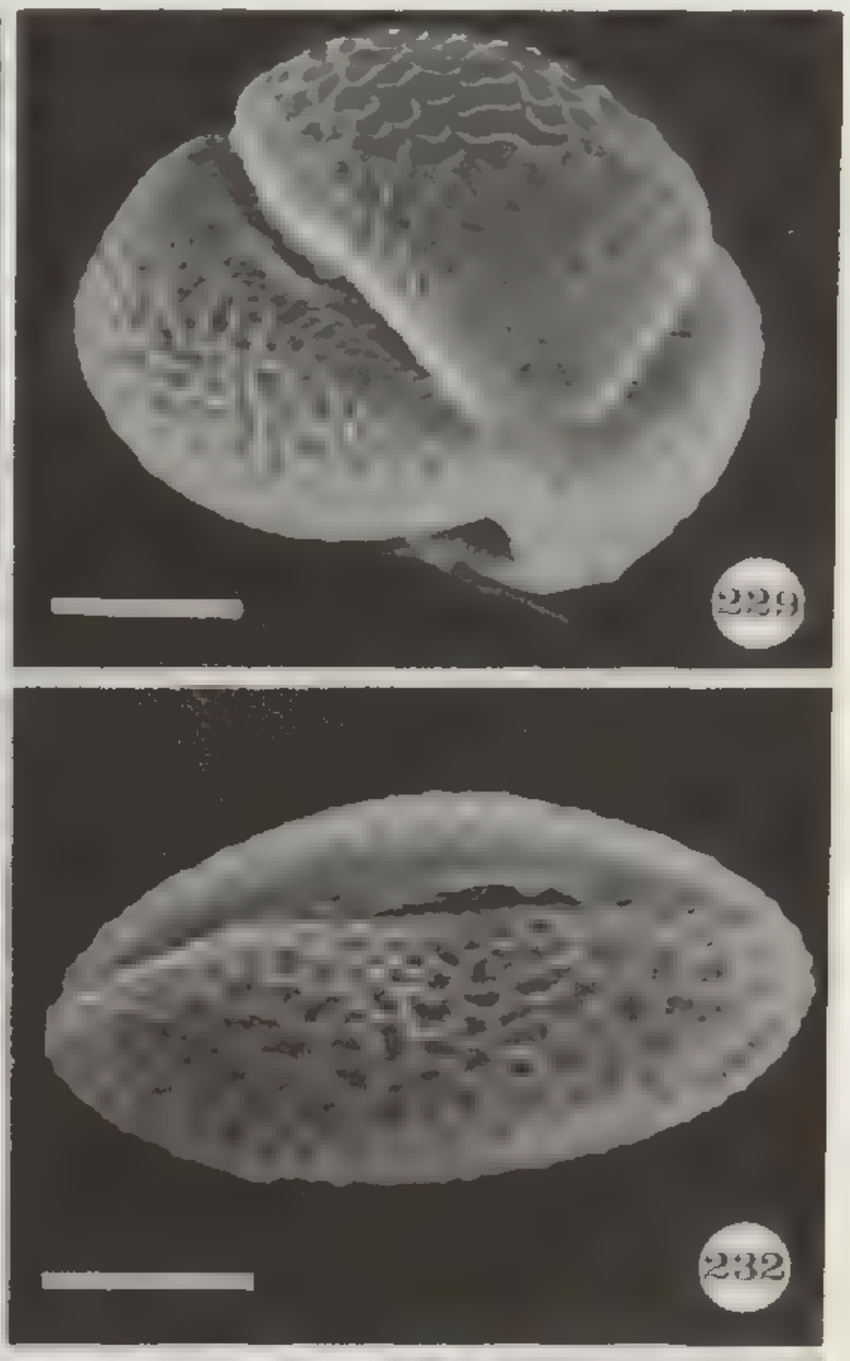


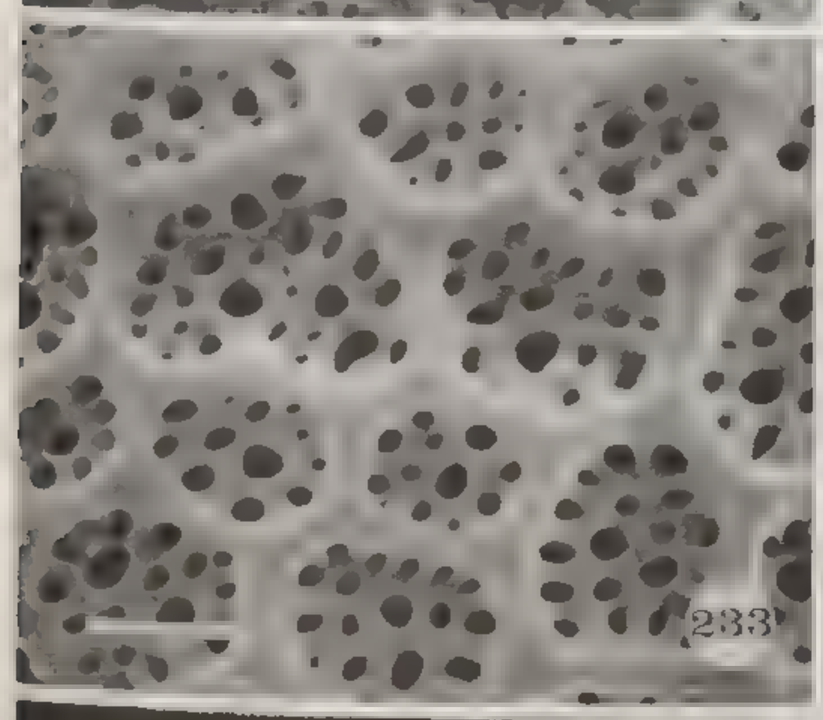
FIGURES 197–211. Pollen of Lamioideae: *Stachyopsis*, *Stachys*, *Stenogyne*, and *Sulaimania*.—197–199. *Stachyopsis oblongata*.—200, 201. *Stachys riddellii* (*Cantino 1229*).—202–204. *Stachys sylvatica*.—205, 206. *Stenogyne haliakalae*.—207, 208. *Stenogyne kamehamehae*.—209, 210. *Stenogyne purpurea*.—211. *Sulaimania otostegioides*. Scales = 1 μm (198, 199, 201, 203, 204, 205, 206, 208, 209, 210, 211); 2.5 μm (197, 200, 202); 5 μm (207).

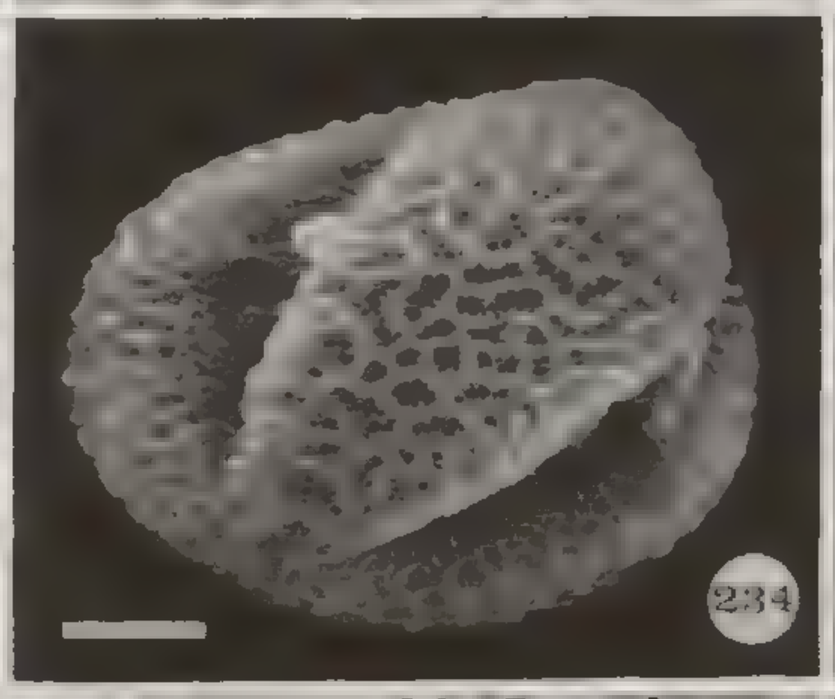
FIGURES 212–226. Pollen of Lamioideae (*Suzukia*, *Synandra*, *Thuspeinanta*, *Wiedemannia*) and genera of uncertain affinities (*Anisomeles*, *Eurysolen*). —212, 213. *Suzukia luchuensis*. —214, 215. *Synandra hispidula* (*Hammer 6*).—216, 217. *Thuspeinanta persica*.—218, 219. *Wiedemannia orientalis* (*Kuntay 48*).—220. *Anisomeles heyneana*. 221, 222. *Anisomeles indica* (*Chun & Tso 43882*).—223. *Anisomeles malabarica*.—224, 225. *Anisomeles salvifolia*. 226. *Eurysolen gracilis*. Scales = 1 μm (213, 214, 215, 217, 219, 220, 222, 223, 225, 226); 2.5 μm (218); 5 μm (212, 216, 221, 224).

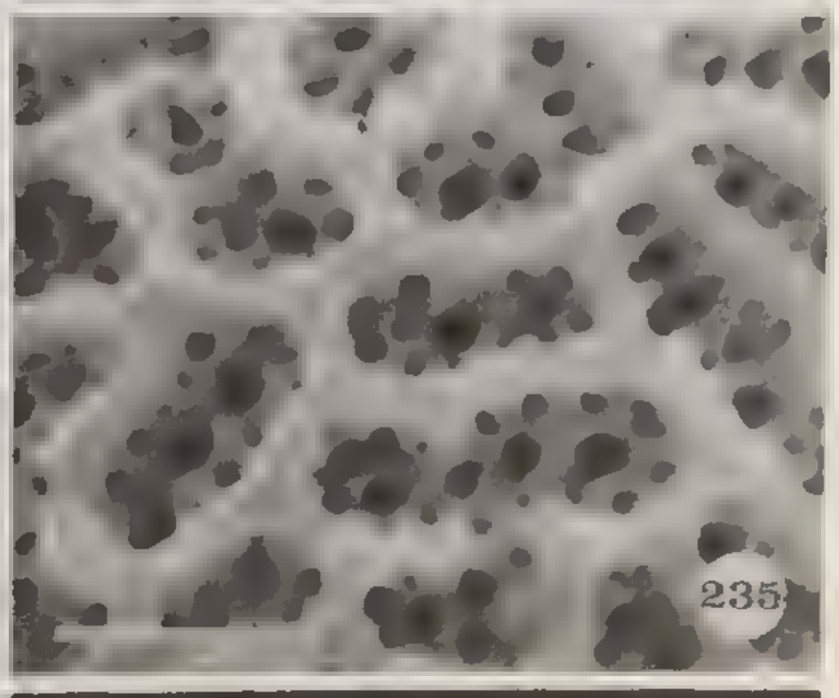


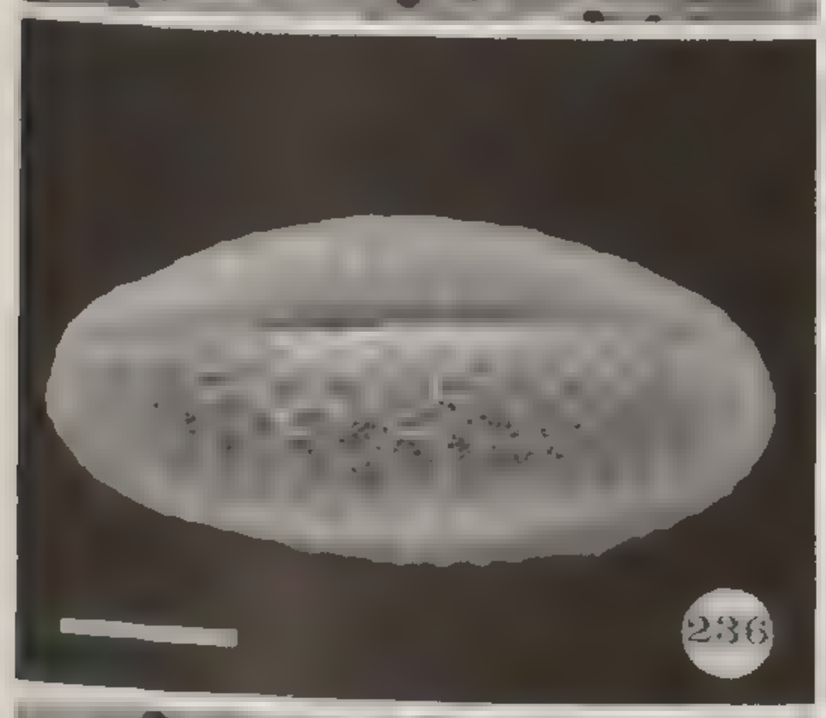


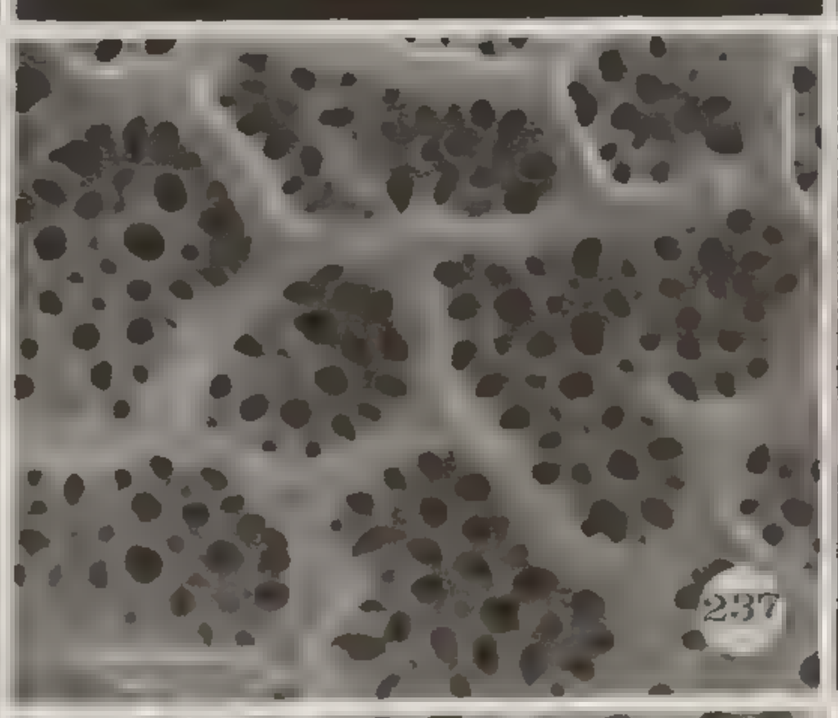


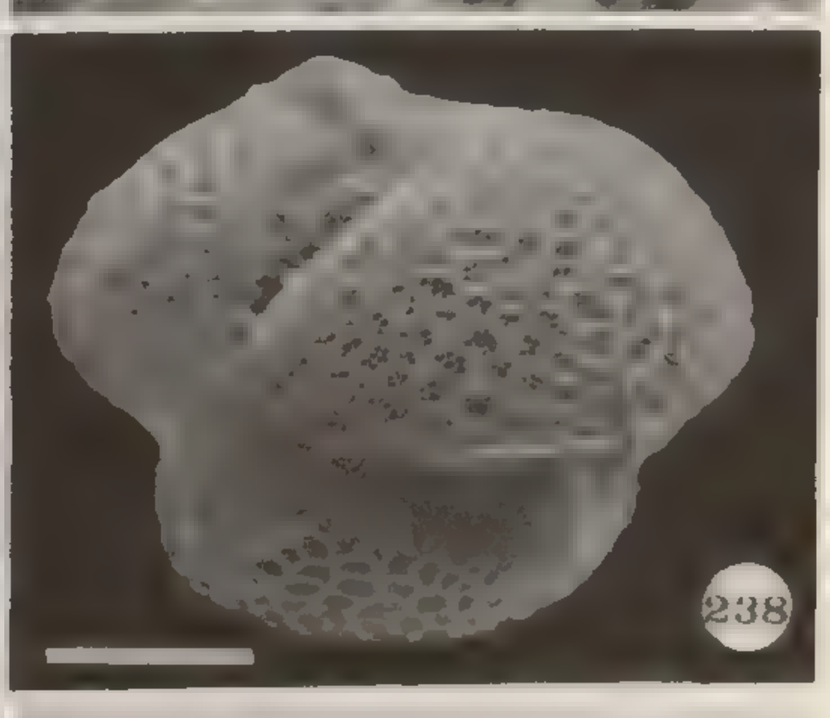


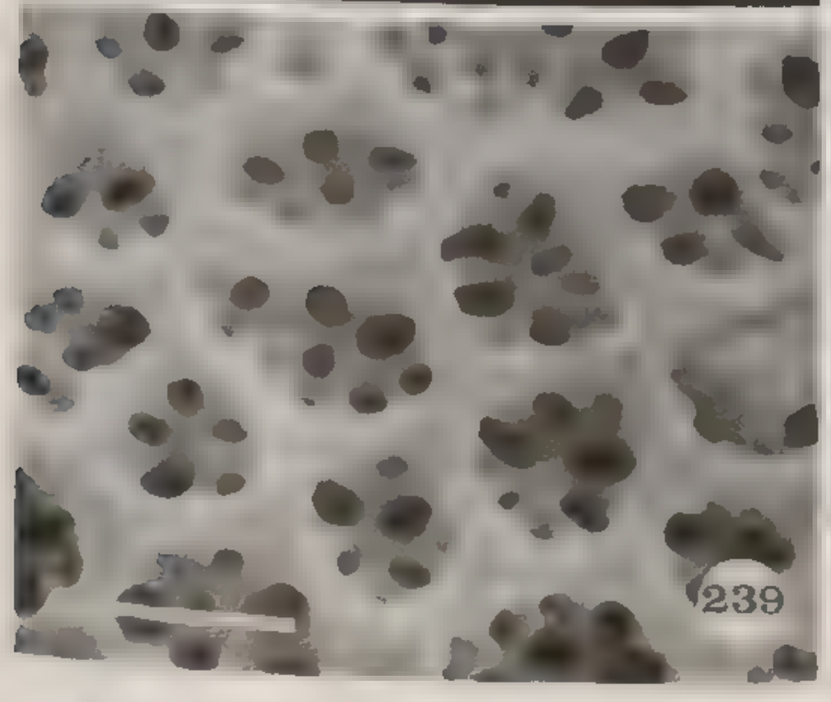


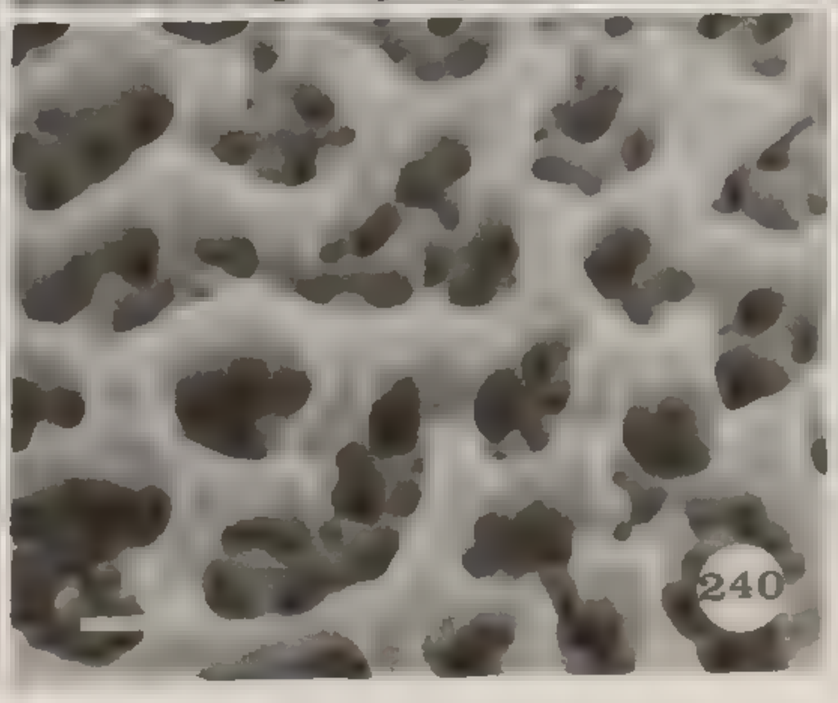


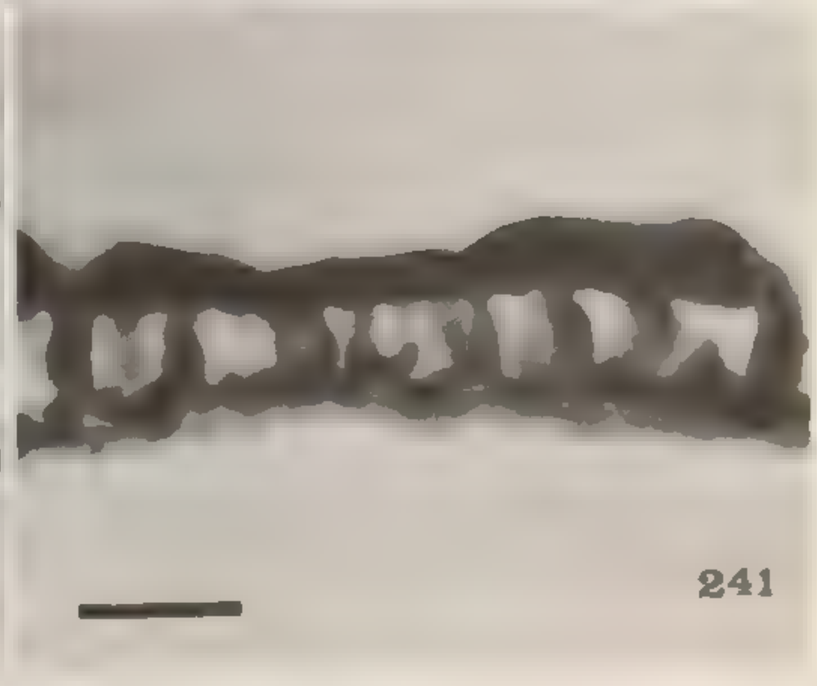




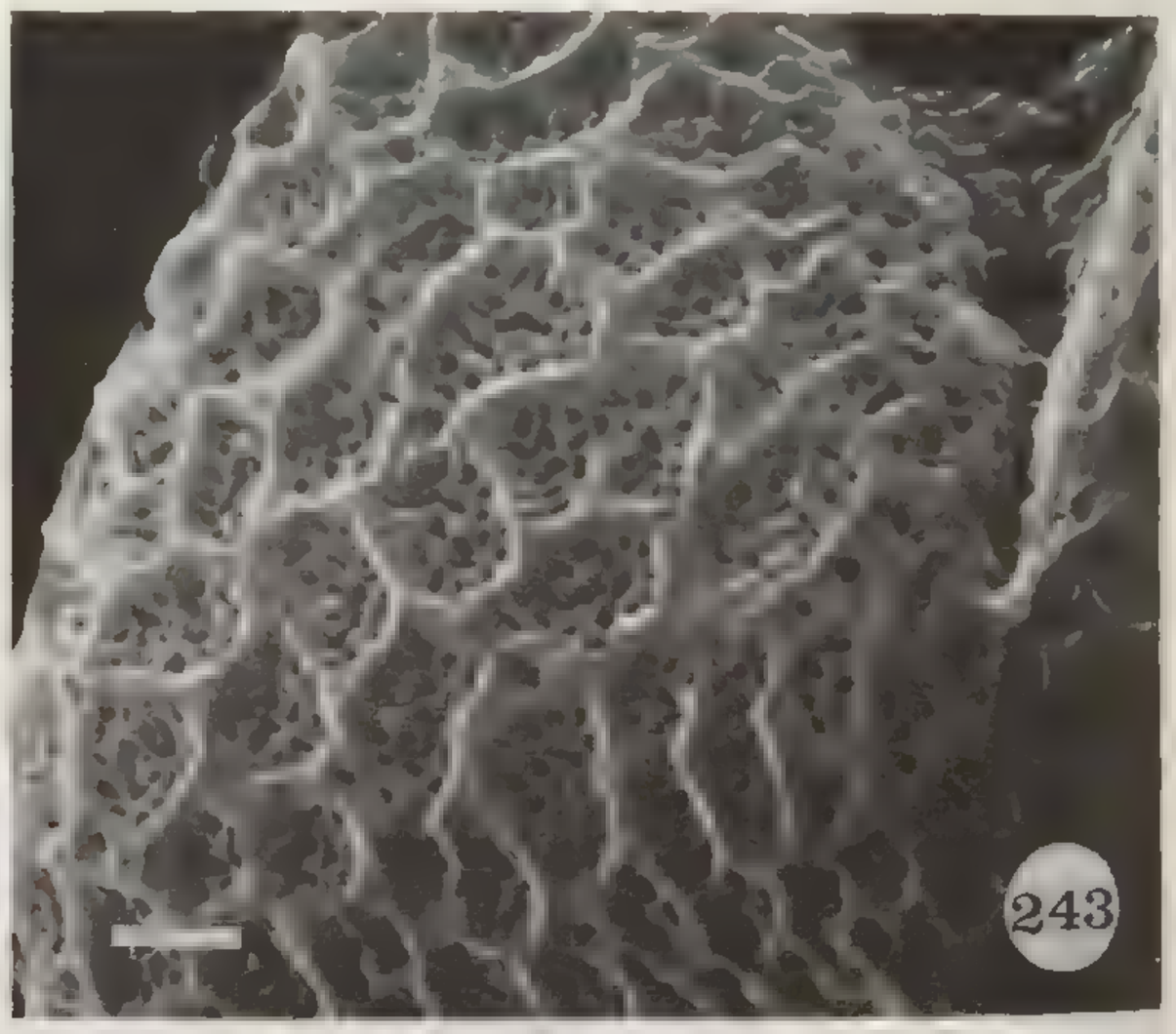


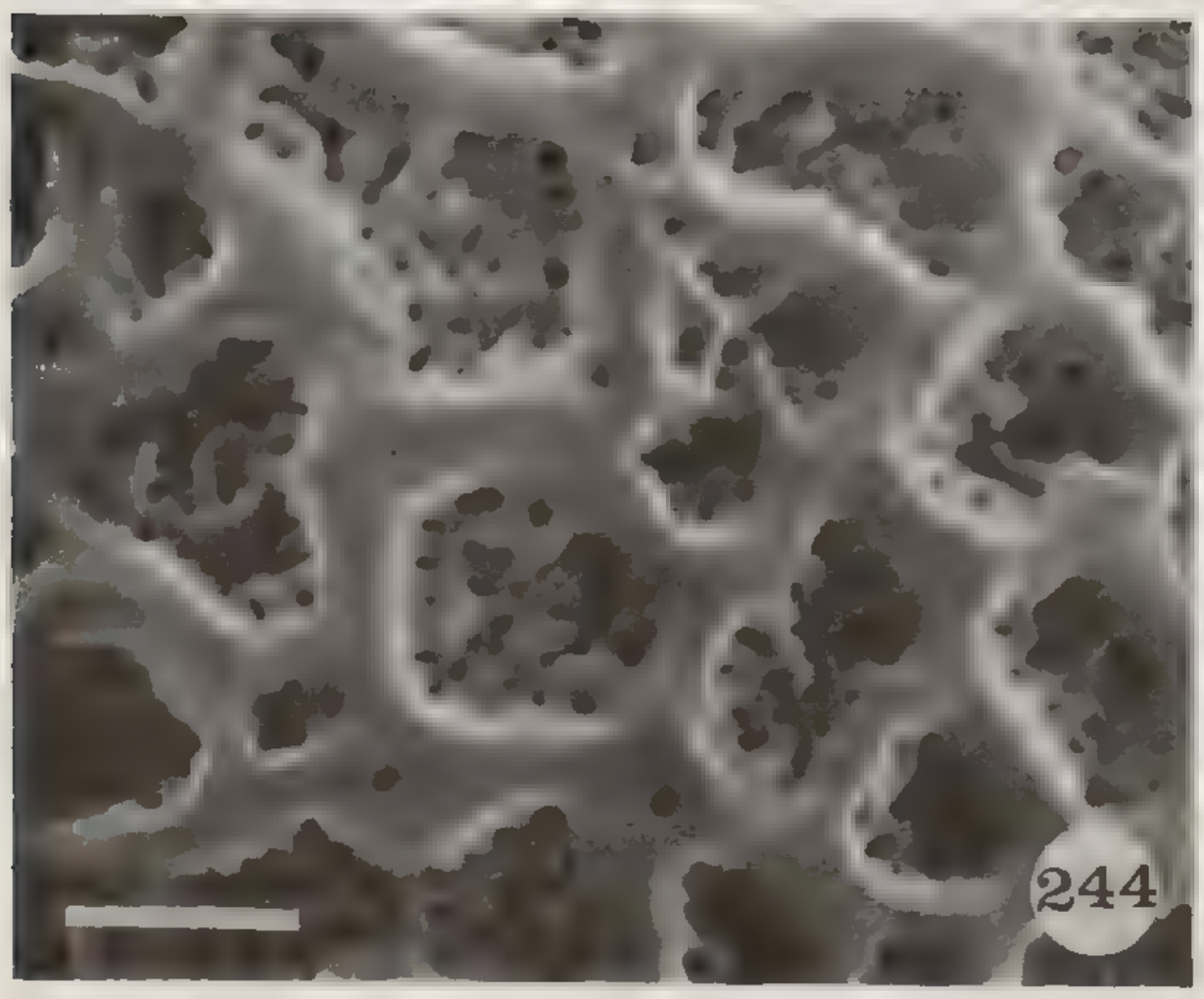


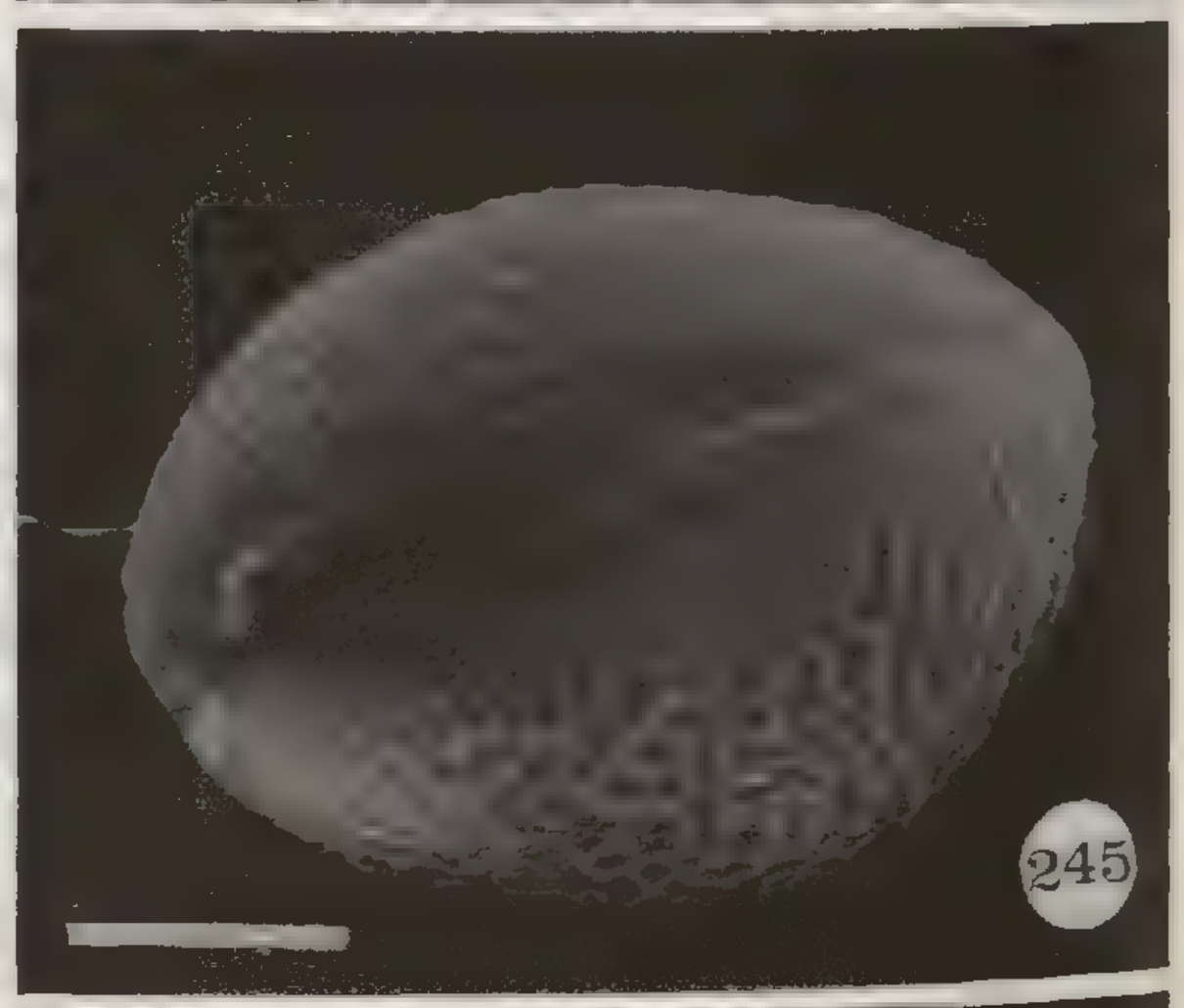


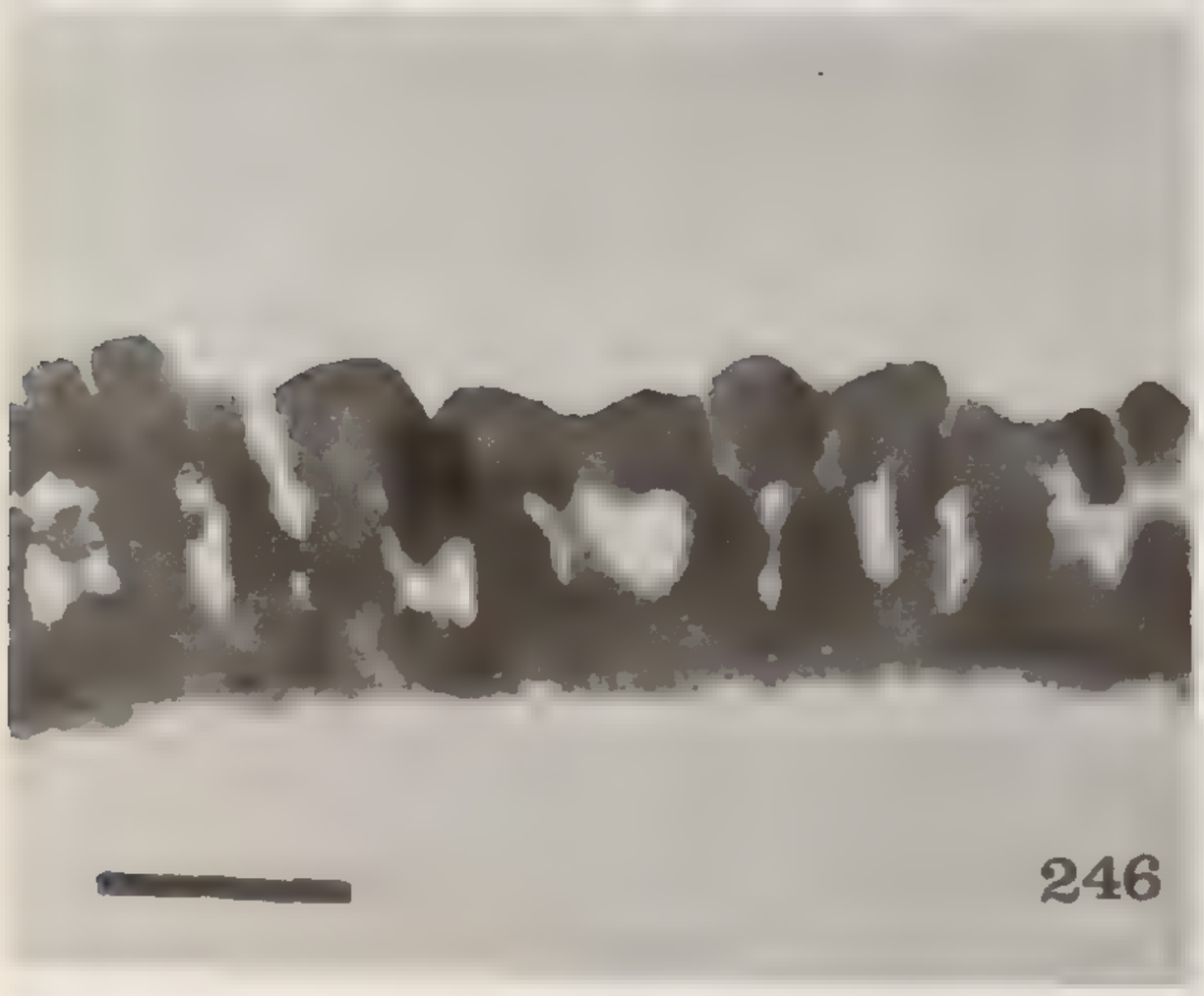


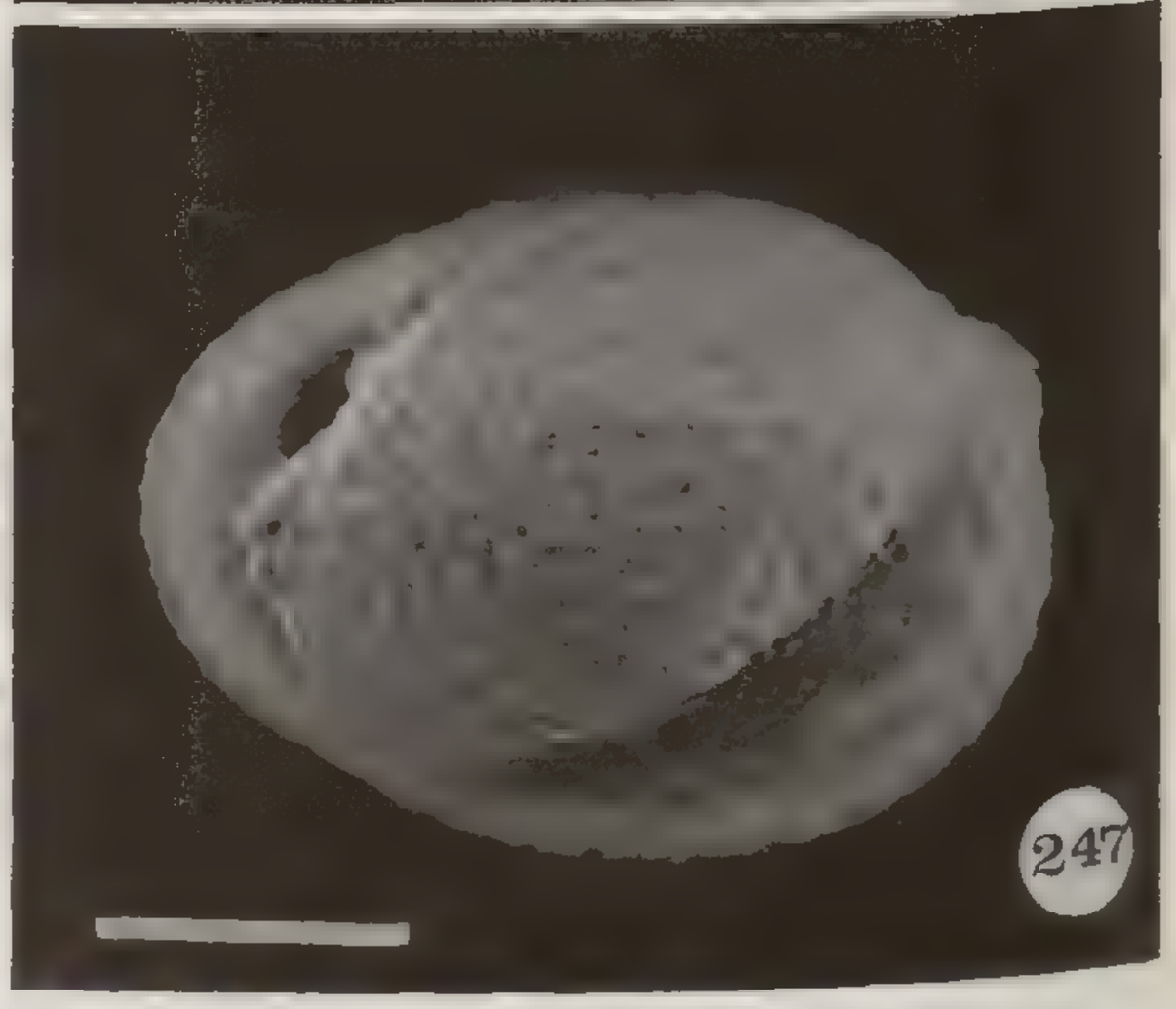
FIGURES 227–241. Pollen of Pogostemonoideae: *Pogostemon* and *Colebrookea*. — 227, 228. *Pogostemon brachystachyus*. — 229, 230. *Pogostemon cablin*. — 231. *Pogostemon cruciatus*. — 232, 233. *Pogostemon glaber*. — 234, 235. *Pogostemon myosuroides*. — 236, 237. *Pogostemon plectranthoides*. — 238, 239. *Pogostemon yatabeanus*. — 240, 241. *Colebrookea oppositifolia*. Scales = 0.5 μm (240, 241); 1 μm (228, 230, 231, 233, 235, 237, 239); 2.5 μm (234); 5 μm (227, 229, 232, 236, 238).











FIGURES 242-247. Pollen of Pogostemonoideae: *Comanthosphace*, *Leucosceptrum*, and *Rostrinucula*.—242, 243. *Comanthosphace japonica* (*anonymous*).—244. *Comanthosphace japonica* (*Ohashi & Murata s.n.*).—245, 246. *Leucosceptrum canum* (*Rock 6650*).—247. *Rostrinucula dependens*. Scales = 0.5 μm (246); 1 μm (243, 244); 5 μm (242, 245, 247).

THE PHYLOGENY AND CLASSIFICATION OF THE DISEAE (ORCHIDOIDEAE: ORCHIDACEAE)[1]

H. P. Linder[2] and H. Kurzweil[2,3]

ABSTRACT

The subtribal classification of the Diseae (Orchidoideae) is reviewed in light of the available morphological, leaf anatomical, and palynological data. These data are critically assessed, and the more prominent features are illustrated. The data are analyzed cladistically, and the robustness of the various components of the most parsimonious tree is assessed by a bootstrap analysis. Based on the cladistic analysis and the bootstrap analysis, a new classification is proposed for the Diseae. The results of the bootstrap analysis are used to establish the nodes at which formal taxa should be recognized. This classification recognizes five monophyletic subtribes: the Satyriinae, Disinae, Brownleeinae (a new subtribe), Huttonaeinae, and Coryciinae. It is suggested that *Brownleea*, the only genus of the Brownleeinae, may be of hybrid origin, as it shares the autapomorphies of the Disinae and Coryciinae. *Huttonaea* is shown to be more closely related to the Diseae than to the Orchideae, and is consequently included as a subtribe of the Diseae. The new classification is formally presented, and a key to the genera is provided.

The Diseae are a tribe of largely terrestrial African orchids, which include the spectacular *Disa uniflora* Bergius, the morphologically complicated subtribe Coryciinae, and the striking *Huttonaea grandiflora* (Schltr.) Rolfe. There are several subtribal classifications available, none of which have been carefully substantiated in terms of their character support. While some of these subtribal groupings may be monophyletic, recent data indicate that several genera are probably misplaced, rendering other groups paraphyletic.

The taxonomy at the species level has been completely revised for all taxa excluding the extra-South African species of *Disperis* and *Satyrium*, and even for these genera several local revisions have been produced recently. In both the subtribes Coryciinae (Kurzweil et al., 1991) and Disinae (Linder, 1986; Linder & Kurzweil, 1990), there have been attempts at reviewing the generic classification. But there are several indications that the subtribal classification may not be as sound as suggested by Linder (1986). A study of *Huttonaea* (Kurzweil, 1989) indicates certain affinities to the Coryciinae, and a recent study on *Brownleea* (Linder & Kurzweil, in prep.) suggests the same.

The first attempt to subdivide the Orchidoideae (tribe Ophrydeae of Lindley, 1830–1840) was by Bentham in Bentham & Hooker (1883), who recognized four subtribes: Euophrydeae (Serapieae), Habenarieae, Diseae, and Corycieae. The former two are not being considered here. The Corycieae are identical to the Coryciinae, Disperideae, or Disperidinae recognized by Pfitzer (1889), Kraenzlin (1899–1900), Schlechter (1898), Rolfe (1912–1913), Senghas (1973–1974), and Dressler (1981). They defined the Corycieae as having adnate petals and dorsal sepals, with lips fused to the gynostemium bases and often appendiculate, and included *Pterygodium*, *Corycium*, *Ceratandra*, and *Disperis* in the subtribe. The only changes over the past century to this group have been in the delimitation of the genera (for a review and phylogenetic classification, see Kurzweil et al., 1991).

The Diseae of Bentham & Hooker (1883) have had a more complicated history. The authors defined this subtribe by its reflexed anther and the large, subterminal stigma. They included the modern Satyriinae (Senghas, 1973–1974; Dressler, 1981), Disinae (Senghas, 1973–1974; Dressler, 1981), as well as three genera of the Orchideae (*Brachycorythis*, *Schizochilus*, and *Platycoryne*) in the subtribe. Pfitzer (1889) substantially followed Bentham and Hooker, but named the group the Satyrieae. Kraenzlin (1899–1900) removed the

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TABLE 1. A comparison of the tribal and subtribal classifications of the Diseae sensu lato.

Bentham & Hooker (1883)		Diseae		Corycieae
Pfitzer (1889)		Satyrieae		Corycieae
Rolfe (1912–1913)		Diseae		Corycieae
Schlechter (1927)		Disaeinae		Disperidinae
Schlechter (1926)	Satyrieae	Diseae		Disperideae
Senghas (1973–1974)	Satyrieae		Diseae	
	Satyriinae	Disinae		Disperidinae
Dressler (1981)		Diseae		
	Satyriinae	Disinae		Coryciinae

last three genera and placed them, in our opinion, in their correct groupings. This narrower definition of the group was followed by all subsequent authors (Schlechter, 1901; Rolfe, 1912–1913; Senghas, 1973–1974; Dressler, 1981). As Bentham & Hooker's definition of the subtribe is uncannily accurate, their inclusion of these three genera in the Diseae must have been based on inaccurate morphological information. The recognition that there are two subgroups within the Diseae (sensu Schlechter and Rolfe) finds expression in the formal recognition of separate groups (Senghas, 1973–1974; Dressler, 1981).

The first suggestion to combine the Satyriinae, Disinae, and Coryciinae into a single tribe, the Diseae, was by Dressler (1979), but has not been accepted by Szlachetko (1991). Other authors used every single combination possible: these are summarized in Table 1.

Huttonaea has had a checkered history. Bentham & Hooker (1883) placed the genus between *Bartholina* and *Holothrix* in the Habenarieae, while Pfitzer (1889) and Kraenzlin (1899–1900) included the genus in the section Gymnadenieae. This approach was followed by Rolfe (1912–1913). Senghas (1973–1974) and Dressler (1981) separated *Huttonaea* into its own subtribe in the Orchideae, the Huttonaeinae, and noted that it had no close relatives. They placed it in the Orchideae because of its apparently erect anther.

The delimitation of the genera in the tribe has been a persistent problem, and different treatments vary greatly. The original generic delimitations were established by Swartz (1800), and were further elaborated on by Lindley (1830–1840). Subsequent students of the group have generally erected smaller and smaller genera, a tendency that finally culminated in the large number of small genera upheld by Rolfe (1912–1913) in the *Flora Capensis*. This system, however, did not result in a phylogenetically sound classification, as the core paraphyletic genera were retained, and some of the segregated genera were polyphyletic groups based on flower resupination and other striking features. In this way Rolfe upset the more synthetic approach of Schlechter (1901), who recognized very wide genera that were generally monophyletic. The generic limits in the Coryciinae were recently assessed by Kurzweil et al. (1991), and detailed arguments on the monophyly of the genera are presented there. The subtribe Disinae still presents a problem. Lindley (1830–1840) already commented on the difficulty of establishing groups within the broad genus *Disa*, and all attempts at establishing an empirically sound generic classification have failed (Rolfe, 1912–1913; Schelpe, 1966; Linder, 1981a–f, 1986; Linder & Kurzweil, 1990). Although the presently recognized segregate genera are clearly monophyletic, their relationship to the large core genus *Disa* is not clear, and it is certain that the recognition of a distinct genus *Herschelianthe* renders *Disa* paraphyletic. In this treatment the genera as established by Linder (1986) are used, despite the clear evidence that *Disa* is paraphyletic. The generic limits in the subtribe Satyriinae have not yet benefitted from a detailed study. However, Linder (1989) demonstrated the monophyly of *Satyrium* relative to *Satyridium* and showed that both can be upheld. The genus *Pachites*, which comprises two species, is poorly known, due to its great rarity, but there is unpublished information that casts doubt on the monophyly of the genus (Kurzweil, unpublished data), and consequently we treat the two species separately here.

These classifications have been heavily based on floral morphology. However, until recently the floral morphology in this group of orchids has been rather poorly understood. The flowers of tribe Diseae are very complicated and difficult to interpret (Dressler, 1981). Individual species were studied in detail by Trimen (1864), Weale (1873), Bolus (1882), and Marloth (1895), but these authors mainly concentrated on species of subtribe Disinae and their pollination. The first comprehensive description of the flowers of a large number of species

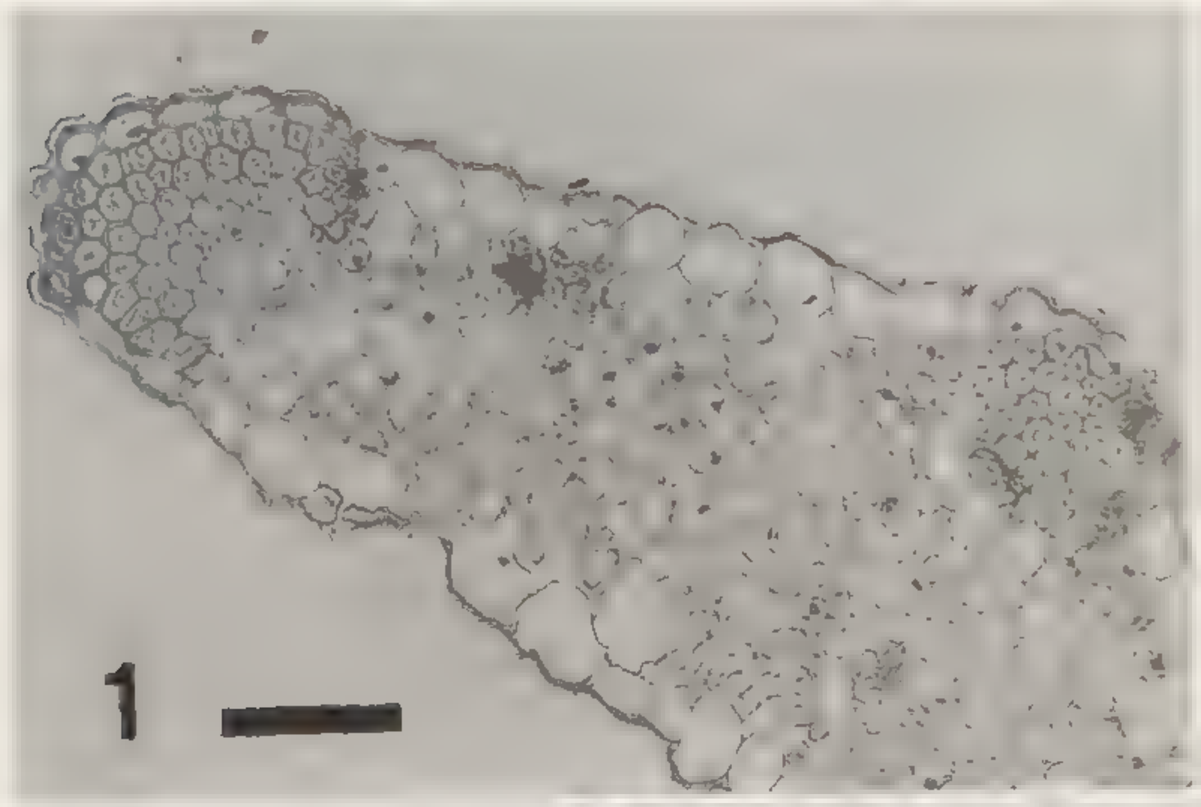
was that of Harry Bolus in his floristic accounts (Bolus, 1888, 1893–1896, 1911, 1913, 1918). Further morphological knowledge was contributed in the floristic and taxonomic studies of Schlechter (1898, 1901) and Rolfe (1898, 1912–1913). The exhaustive study of Vogel (1959) on the floral morphology of various species was frequently regarded as providing the final explanation for the odd flower structures in this group. However, due to the lack of ontogenetic investigations certain structures were misinterpreted. Morphologically significant genera were not dealt with and, consequently, several questions remained unaddressed. In the past five years there has been substantial progress in the knowledge of the morphology and ontogeny of the flowers of the Diseae. Kurzweil (1990) described the Disinae, Kurzweil et al. (1991) and Kurzweil (1991) the Coryciinae, Kurzweil & Linder (1991) some of the *Disperis* species, and Linder & Kurzweil (in prep.) *Brownleea*. In addition, Kurzweil (1989) described the morphology of *Huttonaea* in great detail. Further sources of information have been investigated: Chesselet & Linder (1993) studied the pollinium ultrastructure and Chesselet (1989) reported on the leaf anatomy of the Disinae and Coryciinae. We have extensive unpublished data for the Satyriinae. There are, however, several structures that have not yet been adequately investigated. These include the chromosome complement and the anatomy of the root-stem tuberoids.

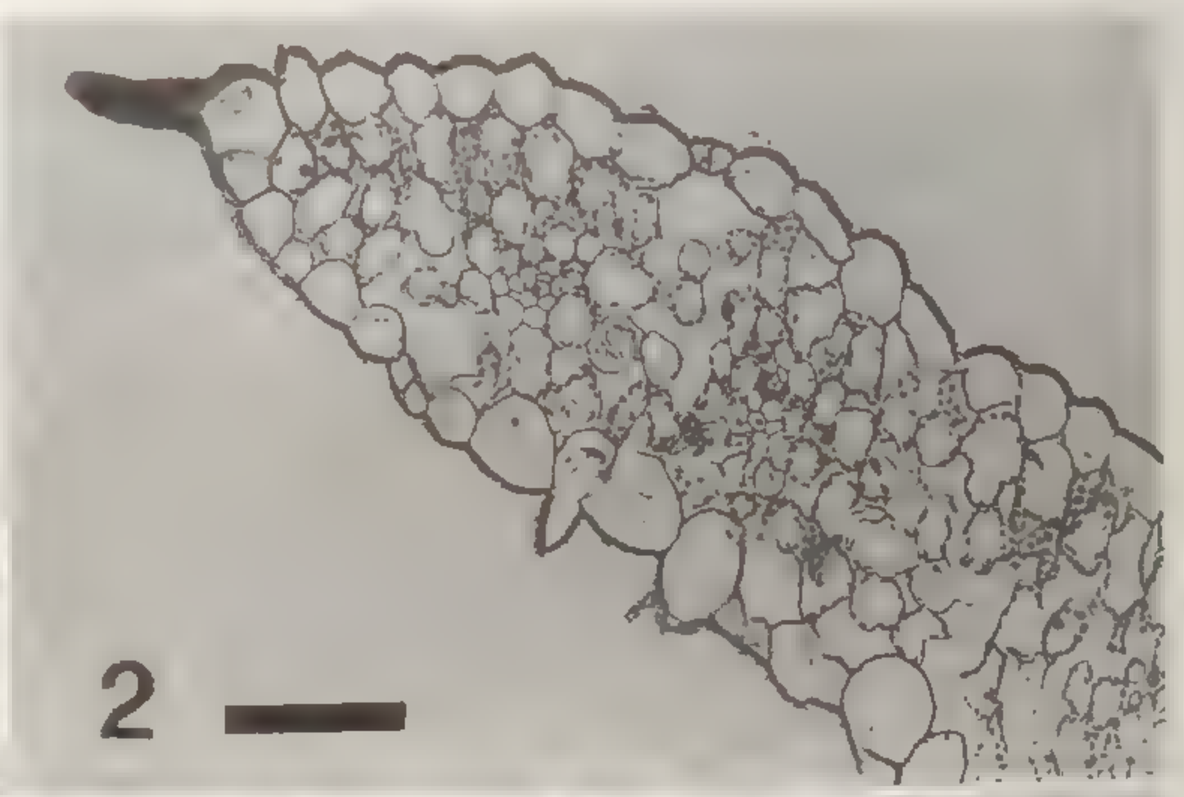
The available data suggest that a careful reconsideration of the suprageneric classification of the tribe Diseae is required. In this study a cladistic analysis of all available data is presented, on which a sound phylogenetic classification for the group can be based.

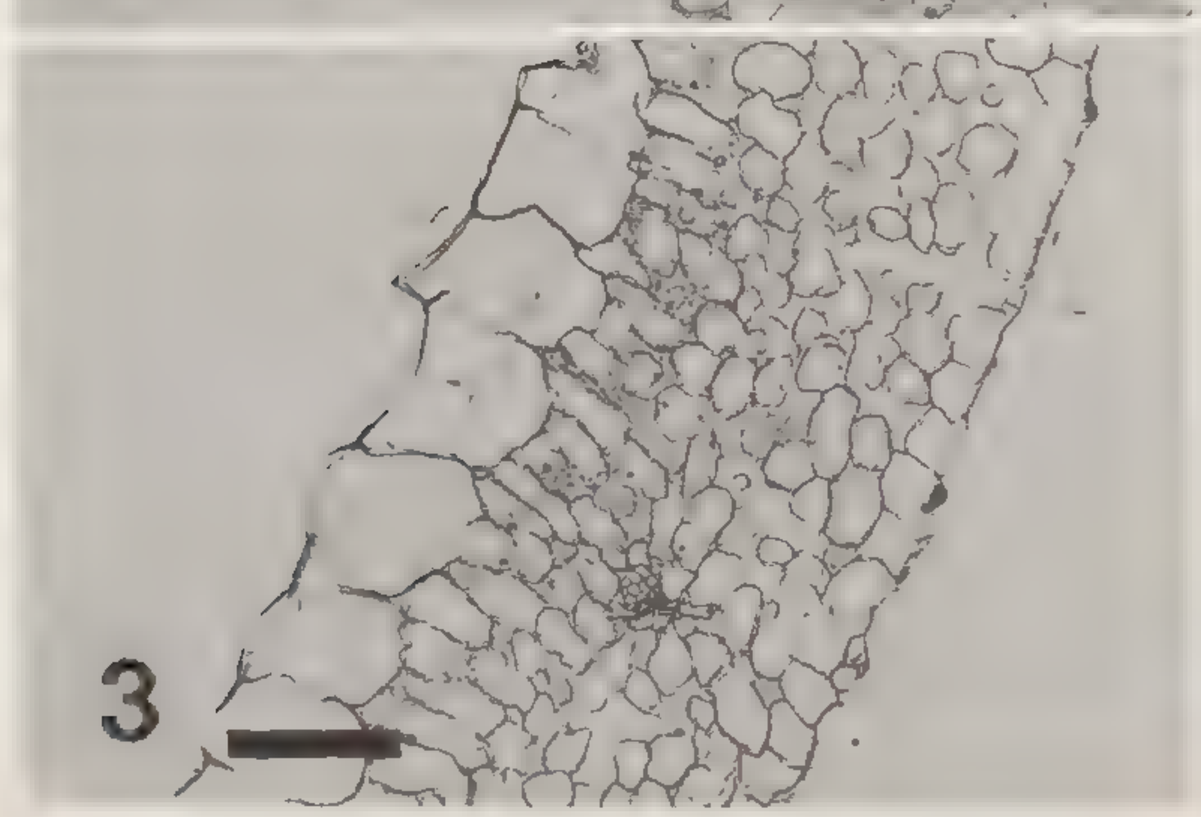
Methods

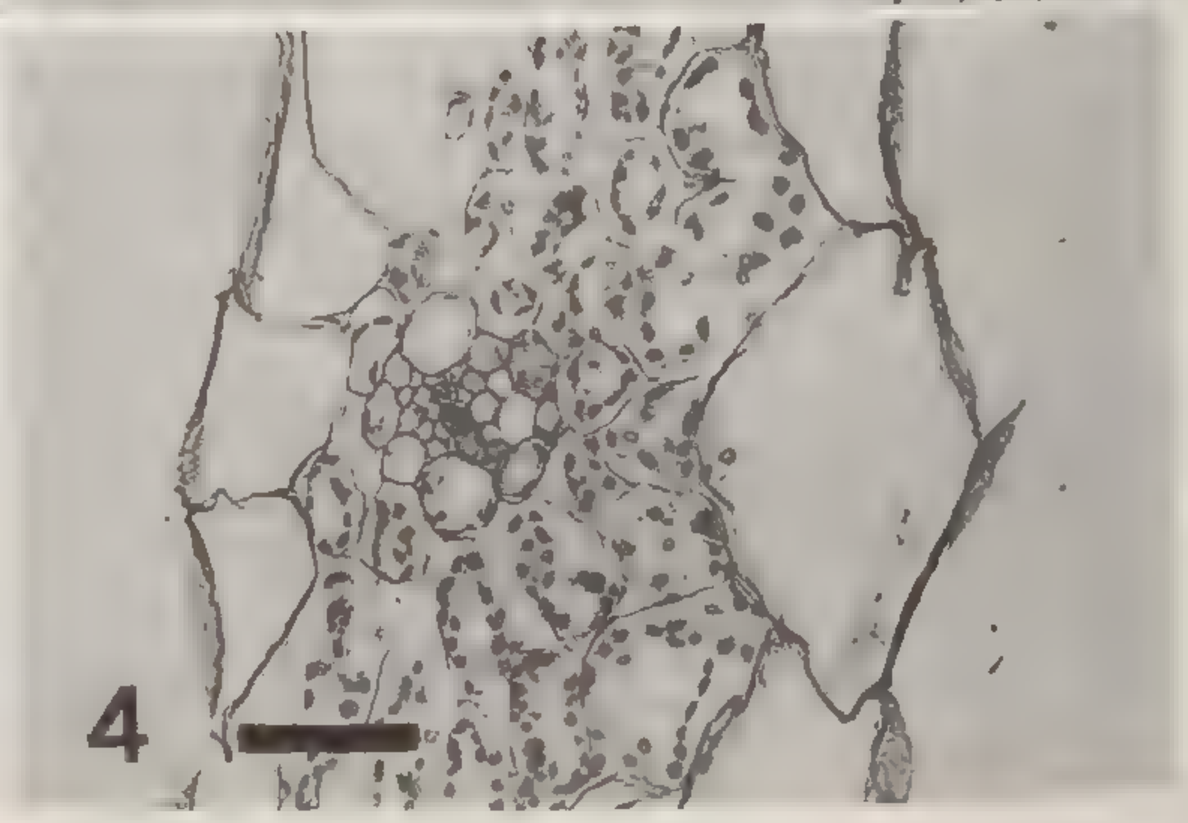
Morphological, anatomical, and palynological data were collected from various publications, and in critical cases new observations were made from the herbarium and pickled collections held at the Bolus Herbarium, University of Cape Town. Vouchers are given in the figure captions. These data were then studied comparatively, scored for the genera, and a maximum parsimony analysis performed, using the "ie*" routine in the Hennig86 (Farris, 1988) cladistic analysis software package. The data were outgrouped to a set of genera belonging to the Orchideae, which differ in the possession of a spurred lip. In order to locate a single more resolved tree, successive weighting was applied (Farris, 1969; Carpenter, 1988). The individual character consistency indices for the three fundamental trees were averaged and used to calculate a weighting for each character, on a scale from 0 to 10. Then the parsimony analysis was rerun to locate the most parsimonious tree. The procedure was repeated until the cladogram stabilized. To test the support for the different monophyletic groups, and the confidence with which they may be proposed, the data set was randomly sampled 100 times, and the analyses rerun (Felsenstein, 1985; Sanderson, 1989; Linder, 1991). For each random sample the consensus tree was calculated from the complete set of shortest equal length trees located by using the "ie*" routine in Hennig86. This was necessary to locate a single tree for each sample to determine the frequency occurrence of each component, a routine which is not explicit in PAUP Version 3.1 (Swofford, 1993). These 100 consensus trees were then scanned, and the frequency of occurrence of each of the components of the most parsimonious tree determined. Although this procedure approximates the "bootstrap" methods of Felsenstein (1985), as implemented by Swofford (1993), it differs in that the components of a selected topology are tested directly, rather than indirectly, by the calculation of a 50% majority rule consensus tree from the set of sampled data sets. Although these analyses do not produce a valid statistical test of the confidence limits for the cladogram (Linder, 1991; Werdelin, 1989), they do give a rough indication of the support implicit in the data set used for each node. The methods used are described by Linder (1991) and Sanderson (1989).

The coding of variable taxa poses some problems. Some of these problems may be due to the terminal groups not being monophyletic, and so incorporating more variation than they should. However, most of the genera have been tested critically for their monophyly (see above) and where there was doubt the problem is clearly delimited (such as in the Disinae), or the genus is broken into its components (such as in *Pachites*). Where monophyletic taxa are variable, there are two ways of coding the variation. If the ancestral condition for the genus has been determined by a cladistic analysis of its species such as in *Brownleea* (Linder & Kurzweil, in prep.) or in the Coryciinae sensu stricto (Kurzweil et al., 1991), this condition is coded for the terminal taxon, because we are interested in the character description of the ancestor of the terminal unit. Where this detailed information is not available, the character is coded as unknown (?) for the genus. Characters for which the evolutionary polarity could not be determined by outgroup comparison because they occur in a small subset of the taxa, but for which ontogenetic









FIGURES 1–4. Leaf anatomy of the Diseae. Scale bar: 50 μm.—1. *Disa oreophila* H. Bolus; note large sclerified caps on the vascular bundles.—2. *Ceratandra atrata* (L.) T. Durand & Schinz; note bristle on leaf margin and small sclerenchyma caps associated with the vascular bundles.—3. *Disa pillansii* L. Bolus; note the differences between the adaxial (on the left side) and abaxial epidermis, and the well-developed palisade layer.—4. *Pterygodium alatum* (Thunb.) Swartz, with the two epidermises similar, and without a mesophyll palisade. Vouchers (PC = P. Chesselet; L = H. P. Linder). 1: *L 3663*, 2. *PC 26*, 3. *PC 22*, 4. *L. 4747*.

data were available, were coded in taxa where the character is missing to reflect the polarity inferred from the ontogenetic data. In several cases a character may be present in the majority of the species, but absent in a few. Where these species are known to be closely related to species with the character, this variation was, as suggested by Stevens (1991), ignored.

MORPHOLOGY

I. VEGETATIVE MORPHOLOGY

There is little variation in the vegetative morphology in the tribe. In *Ceratandra* the perennating organs are swollen roots, while in the remaining genera they are testicular root-stem tuberoids. The only exceptions are some species in *Disa* (Linder, 1981c) in which the tubers may be lost, and the plants propagate by vegetative stolons. In these species there is often a perennial aboveground leafy cover. Although there is variation in the vascularization of the root-stem tuberoids (pers. obs.), the homologies and basic structure of the root-stem tuberoids are at present inadequately understood to interpret the variation, and the database is also still too incomplete.

The leaf anatomy of the Diseae was surveyed by Chesselet (1989) and Kurzweil (in prep.). Although individual species may have very different leaf anatomies (Figs. 1–4), these appear to be homoplasious, and there is no consistent pattern across the tribe. Some genera, like *Herschelianthe* or *Ceratandra*, have distinctive leaf anatomies, but there are no features that combine genera. This

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FIGURES 5–10. Habit and inflorescence structure of various species in the tribe. Scale bars: 5 cm.—5. *Disa cornuta* (L.) Sw.; note robust many-flowered inflorescence. —6. *Huttonaea fimbriata* Rchb. f., inflorescence sparse, leaves broad. 7. *Brownleea macroceras* Sond., inflorescence of 1–2 flowers. —8. *Ceratandra grandiflora* Lindl., many-flowered inflorescence contracted into an almost capitate head. —9. *Pterygodium leucanthum* H. Bolus, relatively sparse inflorescence. 10. *Satyrium candidum* Lindl., robust, many-flowered inflorescence. Sources (HK = H. Kurzweil). 5: *HK s.n.*, 6: *HK 1599*, 7: *HK 1576*, 8: *HK 1226*, 9: *HK 1641*, 10: *Jackson s.n.*

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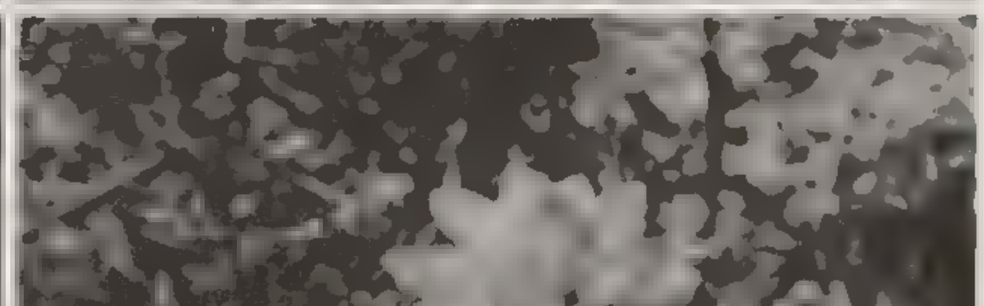
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may not apply in the case of the sclerified leaves of *Herschelianthe*, but the relationship with *Disa* is not clear, and similar leaves occur in some sections of *Disa* (Fig. 1). The occurrence of hysteranthy may be related to the anatomy and texture of the leaves and floral bracts, but this variation is also restricted to within the Disinae, and cannot be properly interpreted until the phylogeny within this subtribe is better understood (Linder & Kurzweil, 1990).

II. INFLORESCENCES

The inflorescences are simple racemes, which vary from many- to single-flowered (Figs. 5–10). However, in most genera some species have numerous flowers, which makes the polarization of this character difficult. It appears likely that a many-leaved, many-flowered plant (e.g., Fig. 5) is the plesiomorphic condition, and, as this occurs in virtually all genera, this does not provide any phylogenetic information above the generic level (see also the discussion on this character in Kurzweil et al., 1991).

III. SEPALS

The involvement of the sepals in the attractive organs of the flower may contain some phylogenetic information. In the Disinae and *Satyrium* the lateral sepals are brightly colored, and may be the largest and most brightly colored floral organs (Figs. 11, 12, 15, 20, 21), while in the Coryciinae sensu stricto (Coryciinae excluding *Disperis*, see Kurzweil et al., 1991) they are green and generally insignificant (Figs. 16, 17, 18). The modification of the sepals to become part of the attraction system of the flowers is difficult to quantify, especially when the flowers are green. Green flowers, in which the sepals differ in texture from the bracts, are also considered modified.

In Disinae the sepals, and sometimes even the petals, are apiculate (Fig. 12). These apicules develop very early in the ontogeny of these parts, and in some species may be very well developed (e.g., *Disa telipogonis* Reichb. f.), although in others they may be obscure (e.g., most species in *Monadenia*). These apicules may be remnants of the unifacial tip of the general monocotyledon leaf structure, consisting of a unifacial tip and bifacial sheath (Kaplan, 1975; Weber, 1980; Rudall, 1990), with the blade developed from either or both of them. Vogel (1959) interpreted the sepals as being homologous to the bifacial sheath and the unifacial tips the remnants of the leaf blades. However, such apicules are absent in the rest of the Diseae, but occur sporadically in many diverse orchid groups. Their polarization is therefore difficult, as theoretically they would be primitive features, but outgroup comparison to the Orchideae indicates that they are synapomorphic for the Disinae.

The lateral sepals are generally unspecialized ligulate to ovate structures (Figs. 11–22). In some genera they contain important autapomorphic characters, or characters that delimit groups within the genera. In *Disperis* the lateral sepals have short conical spurs (Fig. 19), while in *Corycium* they are often papery, and may be partially fused (Fig. 17).

The dorsal sepal is unspecialized (e.g., without peculiar modifications) in the Satyriinae (Figs. 20–22), *Huttonaea* (Figs. 13, 14), and the Coryciinae sensu stricto (Figs. 16–18), but differs in the other genera. In the Disinae (Figs. 11, 12) and in some species of *Disperis* the dorsal sepal is galeate. A spurred dorsal sepal is supposed to be diagnostic for the Disinae, but there are some species without spurs, although these are usually very similar to spurred species (Linder, 1981c, e; Linder & Kurzweil, 1990). It is therefore assumed that the spurs were lost secondarily, and all the genera of the Disinae are coded as having spurred dorsal sepals,

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FIGURES 11–22. Flowers of various Diseae. Scale bars: 5 mm.—11. *Disa erubescens* Rendle; note the large sepals and the narrowly linear lip.—12. *Herschelianthe graminifolia* (Ker Gawl. ex Spreng.) Rauschert; note the broad, ovate lip and the large galeate dorsal sepal.—13. *Huttonaea grandiflora* (Schltr.) Rolfe, with a fimbriate lip and petals. 14. *Huttonaea pulchra* Harv., with spathulate fimbriate petals.—15. *Brownleea macroceras* Sond., with the large lateral sepals and the petals adnate to the dorsal sepal to form the galea.—16. *Ceratandra atrata* (L.) T. Durand & Schinz, with the lateral sepals arching forward and the large hornlike anther thecae.—17. *Corycium crispum* (Thunb.) Sw.; note the large galea constructed largely of the petals.—18. *Pterygodium inversum* (Thunb.) Sw. with a large galea constructed largely from the petals; note that in this species the flowers are not resupinate.—19. *Dispersis paludosa* Harv.; note the spurred lateral sepals.—20. *Satyrium erectum* Lindl., with the lip modified into a two-spurred galea, and the petals and sepals forming the landing platform at the entrance to the galea.—21. *Satyrium odorum* Sond., showing the entrance to the galeate lip, with the upper margin recurved.—22. *Pachites adpressa* Lindl.; note the very simple perianth. Sources (HK = H. Kurzweil). 11: *HK 1404*, 12: *HK 1069*, 13: *HK 1591*, 14: *HK 1623*, 15: *HK 1576*, 16: *Jackson s.n.*, 17: *Jackson s.n.*, 18: Darling Wild Flower Show 1986, 19: *Drewe s.n.*, 20: *Jackson s.n.*, 21: *HK 852*, 22: *Burger s.n.*

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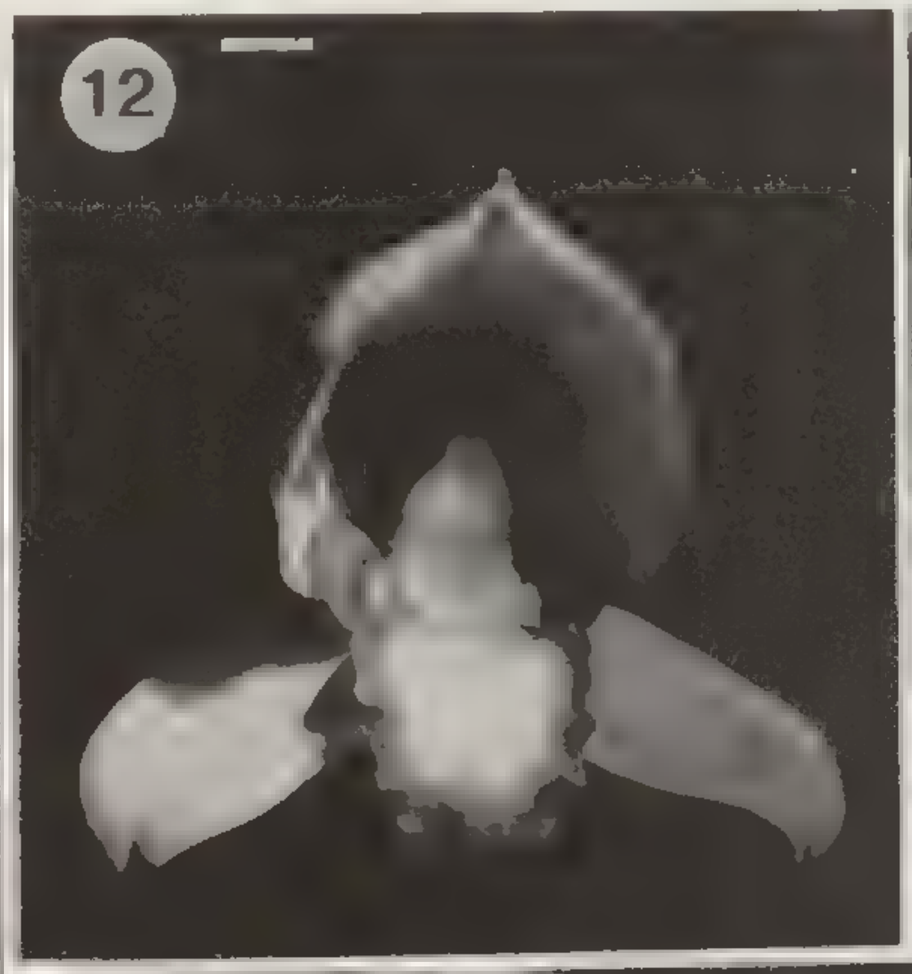
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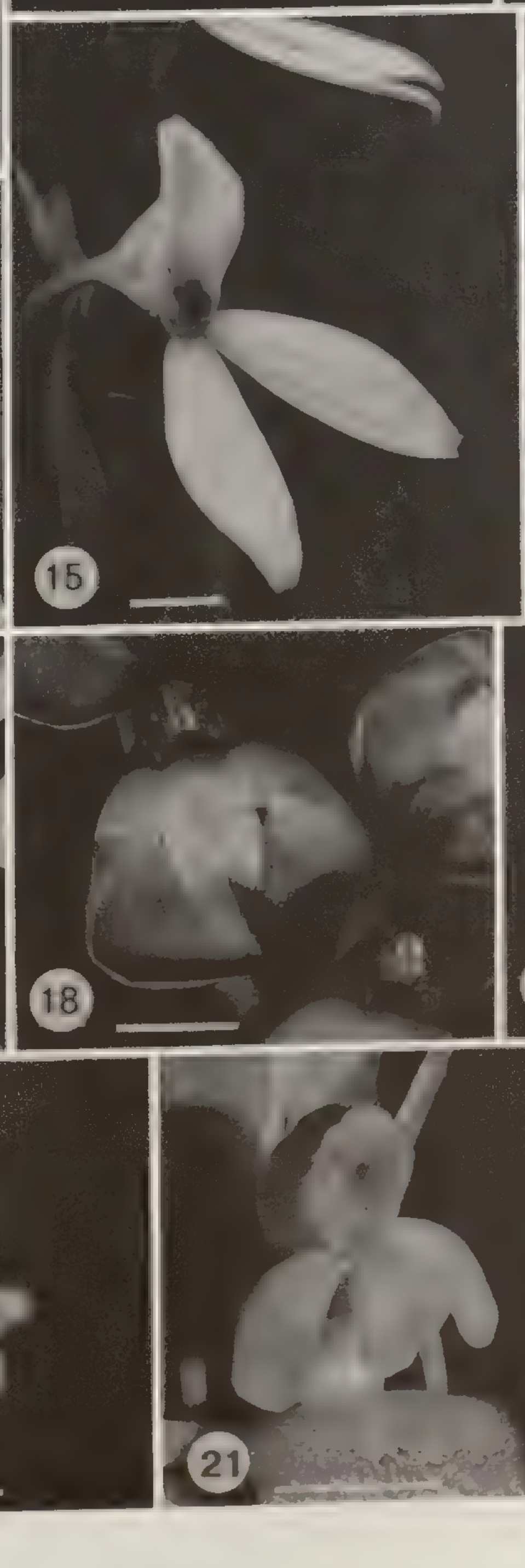
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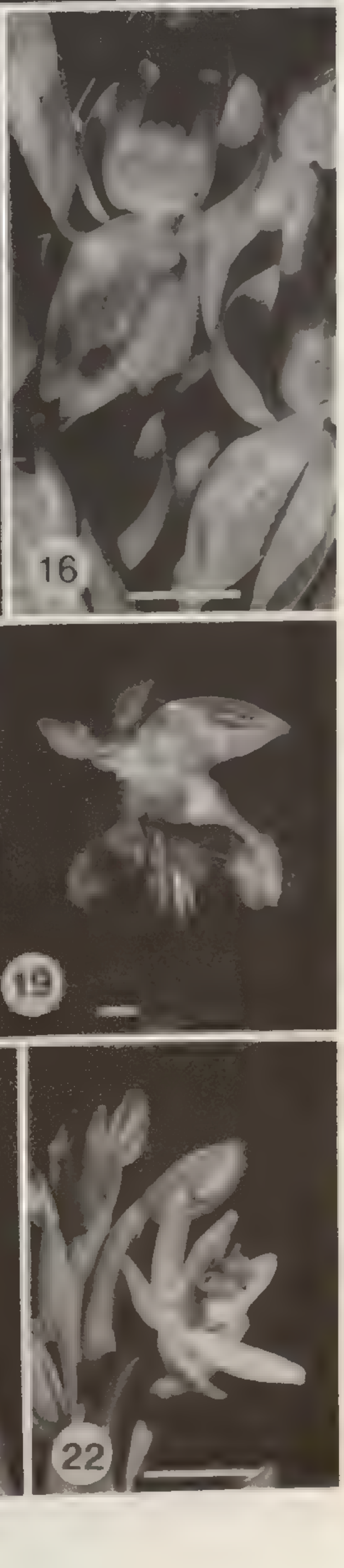
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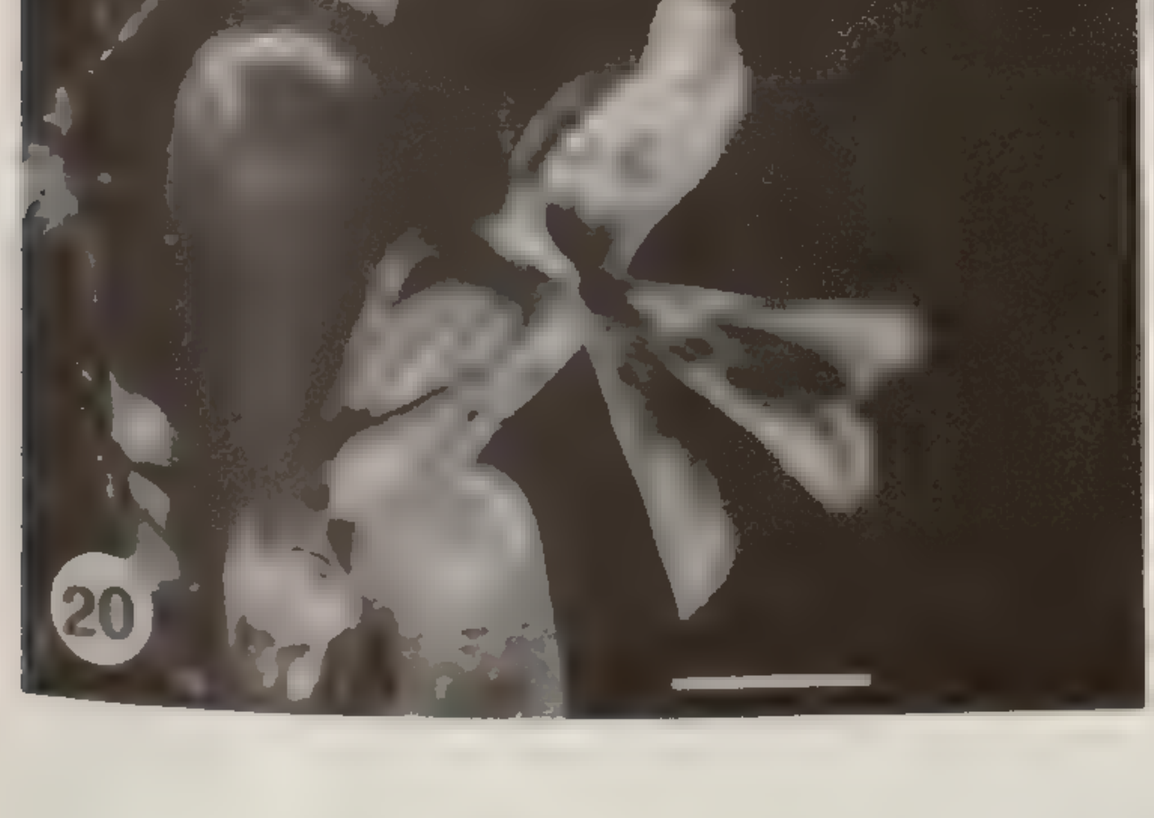
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following the guidelines suggested by Stevens (1991). However, the situation is more complex in *Disperis*, where only a minority of the species bear dorsal sepal spurs. As there is as yet no general cladogram available for the genus, it cannot be inferred whether the presence or absence of spurs is ancestral, nor can the frequency of occurrence argument be used in this case, because it is not clear whether these spurs were lost secondarily or gained independently from the spurs in the Disinae. *Disperis* has therefore been coded as unknown for this character. In the rest of the Coryciinae, the dorsal sepal is not generally galeate and, although it may be concave and form a galea in combination with the petals, it is usually the smallest of the organs involved. It may be that once a deeply concave or galeate dorsal sepal evolves, the step toward a saccate or spurred structure is relatively small, and this may account for the parallel evolution of dorsal sepal spurs in the Disinae and in *Disperis*. Comparison with the cladogram would also indicate a parallel evolution in *Brownleea*, in which the dorsal sepal is a slender organ. This is an exception to the above theory. It is evident that spurred dorsal sepals evolved several times in the Diseae, and as this character has generally been stressed in the subtribal classifications, it may have contributed to the persistent misclassification of *Brownleea*.

IV. PETALS

The petals are very variable in the tribe (Figs. 11–22) and have been found useful at the infrageneric level in the Disinae (Linder, 1981a–e; Linder & Kurzweil, 1990). In the Coryciinae and *Brownleea* the petals are adnate (postgenitally fused) to the dorsal sepal, and the three structures combine to form the galea (Figs. 15–19). This is also found to a lesser extent in the Orchideae, especially in *Cynorkis*. There is extensive variation in the degree of contribution of the petals and the dorsal sepal to the galea, especially in *Disperis*. In some species the petals are simple lorate to linear structures, with the dorsal sepal forming the bulk of the galea (Fig. 19), while in other species the dorsal sepal is a simple, linear structure, essentially only forming the keel of the galea, while the petals form the bulk of the hood (Figs. 17, 18).

In the Disinae and *Brownleea* the base of the petals is fused to the gynostemium. This fusion may be insignificant, or in *Disa* sect. *Aconitoideae* may be in the form of a prominent ridge. Kurzweil (1990) has substantiated Schlechter's (1901) opinion that the fusion keel is derived, at least partially, from staminodes. The presence of various lobes on the petals is useful at specific, sectional, and possibly in some cases generic level, but its presence is rather variable in most genera, making it of little use for suprageneric analysis. Basal anterior lobes have been used to define the sections in the large genus *Disa* (Linder, 1981c), and apically bilobed petals occur in the majority of the species of *Disa* sect. *Micranthae* (Linder, 1981f; Linder & Kurzweil, 1990).

Huttonaea has very peculiar petals, which are clawed, with a saccate blade and a fimbriate margin (Figs. 13, 14). The apices of the fimbriae appear to be glandular (Kurzweil, 1989).

Biologically, the petals in the Disinae appear to function to direct the pollinator into the dorsal sepal spur, in the Coryciinae they form the galea, and in the Satyriinae they form part of the landing platform. The role of the fimbriate petals in *Huttonaea* is not clear, and it is possible that the glands offer a reward for the pollinator.

Frequently associated with this formation of the petals plus dorsal sepal galea is the presence of extraordinarily strongly developed petal nerves. The degree of development of such "petal nerves" is variable, and they are missing in many species. However, although such "petal nerves" have been recorded in various genera of other subfamilies of the orchids, they have a restricted distribution in

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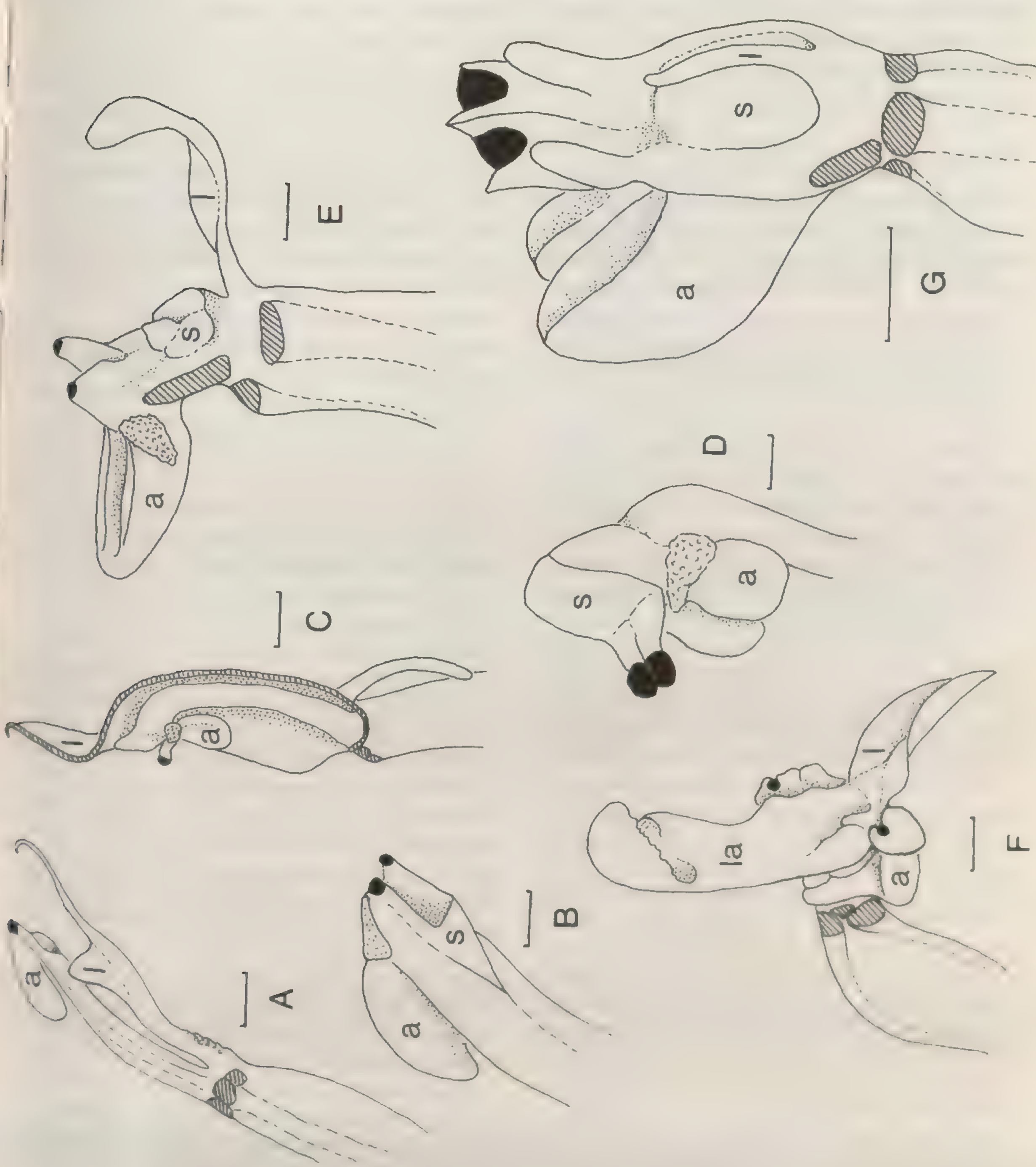
FIGURE 23. Variation in the gynostemium structure in the Diseae, showing only the gynostemium and lip. Cut surfaces are indicated by hatching, the viscidia are black; a = anther, s = stigma, l = lip and la = lip appendage. Scale bars: B, D, E, G: 1 mm, A, C, F: 2 mm. A, B. *Pachites bodkinii* H. Bolus.—A. Gynostemium and lip; note the long column-part and somewhat three-lobed lip.—B. Details of gynostemium apex, showing the reflexed anther, two rostellum lobes and the auricles at the apex of the rostellum lobes. C, D. *Satyrium erectum* Swartz.—C. Gynostemium and a half-section of the galeate lip, showing one of the two spurs.—D. Details of the gynostemium apex; note the flaplike stigma.—E. *Disa tripetaloides* (L.f.) N.E. Br., gynostemium with the horizontal lip, and showing the vertical scar where the petal was attached to the gynostemium.—F. *Pterygodium acutifolium* Lindl., showing the massive erect lip appendage, gynostemium with the anthers widely separated, and the viscidia carried to the sides of the lip. G. *Brownleea recurvata* Sond., showing the lip broadly fused to the base of the stigma, with a narrow erect limb in front of the stigma, and the large fingerlike auricles. Sources. A, B, *Burger s.n.* C, D, *Hall 1031*. E, *Linder 1670*. F, *Linder 1589*. G, *Linder 1767*.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the Diseae, and may therefore be informative despite their occasional absence in some of the groups in which they occur. The polarization of the character on the tree is not unequivocal, as there have been three parallel gains in this character, as compared to four losses. The polarization has therefore been determined by the distribution of the character in the outgroup.

V. LIP

The lip is the most complex perianth member in most orchid groups. It usually makes the orchid flower zygomorphic and often has complex lobes and excrescences. Consequently it has been suggested (e.g., Darwin, 1888) that the lips are morphogenetically complex organs, consisting of an inner tepal and the staminodes. This hypothesis is no longer entertained because of the lack of supporting evidence (Dressler, 1981). Although the lip in the Diseae is enormously variable and often extraordinarily complex, it is very different from the "typical" orchid lip, in that it rarely shows three lobes, rarely has lip-calli, and never has a single median spur (Fig. 23).

The orientation of the lip is variable. In the Orchideae and in some groups of the Diseae the lip is orthotropous: it continues, at least at the base, in the same direction as the axis of the flower. This is particularly evident in the Orchideae with median spurs on the lips, where the spur is parallel to the ovary, and essentially in line with the lip blade. In the Satyriinae the lip is also orthotropous (Fig. 23C). In the Coryciinae and *Brownleea* the lip is also in line with the axis, at least at the base, where it is generally fused to the gynostemium (Fig. 23F, G). In the Disinae excluding *Schizodium*, however, the lip is reflexed at the base, so that it is held at right angles to the axis of the flower (Fig. 23E). A similar situation is found in *Huttonaea* (Figs. 13, 14). In the Disinae the lip is a simple structure, without any outgrowths, usually without lobing, and not fused to any other organs (Fig. 11). It is usually a linear to lorate organ (e.g., *Disa uniflora*), although it may be rarely ovate (*Disa ferruginea* (Thunb.) Sw., *Herschelianthe graminifolia* (Ker Gawl. ex Spreng.) Rauschert, Fig. 12), variously lacerated (*Herschelianthe barbata* (L.f.) N.C. Anthony), clawed (*Herschelianthe multifida* (Lindl.) Rauschert), lobed (*Herschelianthe spathulata* (L. f.) Rauschert), or divided into a hypochile, mesochile, and epichile (*Schizodium*). In *Satyrium* (Figs. 20, 21) and *Satyridium* the lip is galeate and has two spurs. These spurs are obsolete or highly reduced in a few species, but these are almost certainly secondary losses, as the species concerned are clearly related to species with bi-spurred lips. In *Pachites* the lip is very simple, as in the Disinae, while in *Huttonaea* it is broad and fimbriate. In *Brownleea* the lip has a broad base which is fused to the base of the gynostemium, and a tiny linear blade which is erect in front of the rostellum (Fig. 23G).

The lip of the Coryciinae is truly complex. The blade is variable in shape, ranging from linear to triangular to three-lobed and from medium-sized to large. In *Evotella* and *Ceratandra* the lip blade is characteristically spathulate and anchor-shaped (Kurzweil et al., 1991). The base of the lip is almost always fused to the base of the gynostemium. The lip also bears an appendage that is found in the same position as the median adaxial stamen A3 (which is lost in orchids) (Fig. 23F), and this might suggest a derivation from such a staminode (Pfitzer, 1889). However, ontogenetic evidence obtained in various Coryciinae clearly suggests that the lip is of the same nature as the petals (Kurzweil, 1991). The peculiar lip appendage of the Coryciinae is initiated late in the ontogeny. Apparently, the lip appendage of the Coryciinae is merely an outgrowth of the lip as also found in numerous other orchids. This appendage is probably primitively bilobed (Kurzweil et al., 1991; Kurzweil & Linder, 1991), but in many groups there is little trace of the bilobed origin, and in *Corycium* it forms a massive shield over the anther and rostellum (Kurzweil et al., 1991).

The function of the lip in the pollination biology is, like the petals, complex. In *Satyrium* and *Satyridium* it forms the hood and the spurs bearing the nectar; in the Disinae it forms part of the landing platform together with the lateral sepals, and in the Coryciinae it usually bears the oil-bearing attractant for the oil-gathering bees (Steiner, 1989).

VI. GYNOSTEMIUM

The anther is basally reflexed in this group of orchids (Fig. 23). This reflection occurs very late in the ontogeny, directly before anthesis. However, there are exceptions to the rule of the reflexed anther. In *Disa* sect. *Micranthae* and *Pterygodium* sect. *Ommatodium* the anther is always erect, and there is no evidence of any reflection during ontogeny. In the case of *Pterygodium* sect. *Ommatodium*, Kurzweil et al. (1991) postulated that the erect anther is derived from a reflexed anther, and this was supported by their cladistic analysis. In *Brownleea* the anther is basally reflexed, but the apical portion is erect, giving the impression

of an erect anther. The situation in *Huttonaea* is not clear. The anther appears to be erect, but there are some indications that it has a slight tendency to being reflexed.

The anther-cells are generally parallel to each other. *Huttonaea* is exceptional in that the anther cells in these plants diverge toward their bases, while the apices remain proximal to each other. In the Coryciinae, excluding *Disperis*, the anther-cells may still be parallel to each other, but they are far apart, flanking the gynostemium (Fig. 23F). The connective is strap-shaped with the anther-cells situated at the ends of the connective. At its apex, the anther is either broadly rounded, emarginate to deeply split, or has a very short obtuse connective process. In species where the anther-thecae are separated, the median part of the connective is always rounded or somewhat emarginate. A very prominent connective process, resulting in an acute anther, is found in some Orchideae (especially *Serapias*) and is considered the ancestral state for the Orchideae and Diseae by Dressler (1990).

Almost all species have prominent lateral gynostemium appendages (Fig. 23). The situation with regard to their derivation from "basal bulges" (staminodes) and "auricles" (filament appendages) is less clear than in the Orchideae (Kurzweil, 1987b), as their primordia are very obscure in the early ontogeny of most Diseae. However, both structures exist in the tribe Diseae and are prominent in certain species.

In *Disa obtusa* Lindl. the basal bulges are significant during early ontogeny, and later develop into a ridge on the keel connecting the petals with the gynostemium (Kurzweil, 1990). The presence of a similar structure in mature flowers of many Disinae (e.g., Fig. 23E) suggests that this staminodial nature of the keel is the general situation in the subtribe. The auricles develop from significant primordia, and in the adult flower are seated on top of the connecting keel and are fused to the latter and to the rostellum. They are very variable in shape, ranging from small and sculptured to large and comparatively flat.

Mature flowers of the Satyriinae have comparatively large lateral gynostemium appendages next to the anther. During the middle and late ontogeny they are distinctly two-lobed, but significant primordia were not observed in the early ontogeny (Kurzweil, in prep.). In some species the bilobed nature persists in the mature flowers. As detailed ontogenetic studies have not yet been made on this genus, it can only be suspected that the two-lobing of the late-ontogenetic appendages indicates their derivation from staminodes and auricles like in most other Orchideae and Diseae.

A keel connecting the petals with the gynostemium is also present in *Brownleea* (Fig. 23G), and also in this case it may incorporate the staminodes. However, clear ontogenetic evidence was not found in the three species studied (Kurzweil, 1990; Linder & Kurzweil, in prep.). *Huttonaea* species have prominent lateral gynostemium appendages, which appear to be derived from auricles only. In the Coryciinae sensu stricto significant lateral gynostemium appendages are never found in mature flowers, and apparently the staminodes are incorporated into the gynostemium tissue below the rostellum (Kurzweil, 1991), while the central thickened portion of the connective may represent fused auricles. Many *Disperis* species have bi-partite lateral gynostemium appendages (Manning & Linder, 1992; Kurzweil & Linder, 1991), with a smooth and erect portion fused to the lip base and a smaller sculptured horizontal portion on the side of the gynostemium. It is possible that the smooth erect portion is a staminodial structure, and that the sculptured horizontal portion represents the auricle.

The primitive condition of the Diseae and Orchideae seems to be the presence of prominent staminodes that are fused to the gynostemium. Since orchids have probably evolved from ancestors with three abaxial and basally fused stamens, the presence of significant lateral staminodes must be regarded as an ancestral feature, and this is apparently the more general state in the orchid family as it is found in most groups (Kurzweil, 1987a, b, 1988; further references are given there). The extensive keels connecting the petals with the gynostemium as found in *Brownleea* and the Disinae can be regarded as well-developed staminodes and thus as a primitive state, although the formation of the connecting keels is unique and certainly derived. Similar connecting keels are also found in the *Brachycorythis* group (Orchideae). Comparatively large staminode primordia are found in *Disperis fanniniae* Harvey and *Ceratandra atrata*. In the remainder of the Coryciinae, in *Huttonaea* and possibly in the Satyriinae, the staminodes are strongly reduced, which is clearly derived.

Previously the occurrence of auricles (filament appendages) was regarded as a unique character of the Orchideae and Diseae. However, such structures have also been reported from several groups of the "Diurideae" (Dressler, 1986), although the homology of these structures to the auricles of the Orchideae/Diseae needs more research. Auricles

TABLE 2. Variation in the structure of the rostellum in the Diseae.

Taxon	Number of lobes: mature	Number of lobes: primitive	Central lobe	Lateral lobes	Viscidium
Orchideae	3	3	infrathecal tooth	square to elongate	2: lateral lobes
Disa	3	3	infrathecal tooth	square	2: lateral lobes
Herschelianthe	3	3	infrathecal tooth	square	2: lateral lobes
Schizodium	3	3	infrathecal tooth	square	2: lateral lobes
Monadenia	1	1	massive	NA	1: central lobe
Brownleea	2*	2–3	lost or reduced*	elongate, erect	2: lateral lobes
Huttonaea	3	3	massive	minute	2: lateral lobes
Ceratandra	2	2	lost	large, flat, each half covering one theca	2: lateral lobes
Pterygodium	3	1?	small	elongate, twisted	2: lateral lobes
Corycium	3	2–3	small	moderately elongate, strongly twisted	2: lateral lobes
Disperis	3	2?	flat and covering both thecae	elongate, projecting	2: lateral lobes
Satyrium	1(3)	1(–3)	variable	obscure	2: lateral lobes
Satyridium	1	1	massive	NA	1: central lobe
Pachites bodkinii	2	?	lost	massive	2: lateral lobes
Pachites adpressa	3	?	large U-shaped tape	minute	2: lateral lobes

* = exceptions occur; ? = unknown; ( ) = rarely occurring; NA = not applicable.

are certainly the basic condition of the Orchideae and Diseae, and their reduction in the Coryciinae sensu stricto and possibly in the Satyriinae is probably derived.

The rostellum, which is developed from the median carpel apex, as is typical of the orchids, is basically three-lobed. However, the lobes are developed differently in the various groups (Table 2).

In the Disinae the central lobe is folded between the anther cells and varies from relatively small to quite prominent. This is essentially similar to the condition found in many of the Orchideae and may well be the basal condition for the Orchidoideae. *Monadenia* is unique in the Disinae by its massive central rostellum lobe, with minute or absent lateral lobes.

The situation in the Satyriinae is less clear. Generally, the rostellum is less clearly three-lobed than in the Disinae and the Orchideae. The rostellum is either weakly three-lobed or unlobed although emarginate in some species. In several species there is no evidence of rostellar lobing even in the early ontogenetic stages. Within *Satyrium*, there is a wide range of different sizes and shapes of the central rostellum lobe (Summerhayes, 1968; Williamson, 1977), ranging from massive and comparatively flat to fingerlike or to short knoblike. The lateral parts bear the viscidia in lateral or subterminal position. A detailed comparative analysis of the diverse rostellum structures may contribute valuable characters for a phylogeny of the genus *Satyrium*, but our data are not at present adequate for wide-ranging interpretations.

The genus *Satyridium* is characterized by having a median carpel apex/rostellum, which is unlobed throughout the ontogeny and bears a single terminal viscidium in adult flowers. This is an interesting convergence to *Monadenia*. The two species of the genus *Pachites* are very different in their rostellum morphology. *Pachites appressa* Lindl. has a rostellum with small lateral lobes bearing the viscidia and a large U-shaped, straplike central rostellum lobe between them. *Pachites bodkinii* H. Bol. has a rostellum with two elongate and projecting lateral lobes and an obsolete central lobe. A large structure in the position of a central rostellum lobe was consequently also interpreted as such (Bolus, 1893–1896; Rolfe, 1912–1913; Schlechter, 1901; Schelpe, 1966), but has been shown to contain pollen massulae and thus proves to be a pollen sac (Kurzweil, 1993a).

In *Brownleea* the rostellum is three-lobed, although the central lobe is usually strongly reduced or subobsolete. This is already visible in the early ontogeny, as the central rostellum lobe is initiated later than the two lateral ones and is insignificant in all stages. This tendency is also present in *Huttonaea*, in which the rostellum is not deeply three-lobed, and the main portion is derived from the central lobe, while the lateral lobes are minute. The

Coryciinae also show evidence of a successive reduction of the rostellum three-lobing. In *Ceratandra*, the rostellum is flat, deeply two-lobed throughout the ontogeny and covers the thecae on their dorsal sides (Kurzweil, 1991). In *Corycium* and *Pterygodium*, the anther-thecae are far apart, and the rostellum is then developed as a narrow elongate strap between them. While the main portion of the strap is derived from lateral rostellum lobes, a small but distinct median portion is visible in some species, and this is apparently homologous to a central rostellum lobe. Ontogenetically, the rostellum of *Pterygodium* and *Corycium* develops from a shallowly three-lobed, two-lobed, or unlobed median carpel apex. The rostellum of *Disperis* is very different. The lateral rostellum lobes are developed as elongate projecting arms. The central lobe is remarkable in that it is large and flat and covers the anther. It was shown in one species that the rostellum develops from an initially two-lobed median carpel apex (Kurzweil, 1991), but no ontogenetic information is available from other *Disperis* species.

The stigma shows some remarkable peculiarities in this tribe. In the Disinae and Satyriinae the stigmatic surface is developed from the three carpel apices, which is the common situation in the Orchidaceae (Fig. 23D, E). The median carpel apex contributes from between half to somewhat less than one-third of the total stigmatic surface, but this is variable even between closely related species. However, in the Coryciinae, as well as in *Brownleea* (Fig. 23G) and *Huttonaea*, the stigma is made up entirely of the median carpel apex, and the lateral carpel apices remain as small, sterile, vestigial organs (Kurzweil, 1989, 1991; Kurzweil & Linder, in prep.). This derivation of the stigma from the median carpel apex is rare in the orchids, and has only been recorded elsewhere in the Spiranthoideae (Rasmussen, 1982). It should be noted that two species in *Brownleea*, *B. parviflora* Harvey ex Lindl. and *B. mulanjiensis* Linder, have stigmas consisting of all three carpel apices. This may either represent a basal condition for the genus, or a secondary reversal. The situation is analyzed in detail in Linder & Kurzweil (in prep.), and the most parsimonious solution indicates that these two species present a secondary reversal. However, a bootstrap test shows that the alternative solution also gets significant support.

In the Disinae the stigma is distinctly pulvinate and is usually raised on a platform in front of the rest of the gynostemium. In extreme cases the stigmatic surface may have a raised rim along the front margin, so that it faces backwards. Superficially this is similar to the stigma in *Satyrium*. However, in *Satyrium* the carpel apices form two lobes, with the adaxial, receptive lobe derived from the fused lateral carpel apices, while the abaxial lobe represents the median carpel apex and is only basally receptive. In *Satyridium* and *Pachites bodkinii*, the stigma is a small, slightly convex, round pad on the front side of the gynostemium (= facing the lip). In *Pachites adpressa* the stigma is a deep cavity encircled by the U-shaped central rostellum lobe, and is developed on the back side of the gynostemium (= facing the median sepal). The stigma of the Disinae and Satyriinae has been called pseudoterminal by Bentham & Hooker (1883), and Pfitzer (1889) also commented on the often terminal position of the stigma on the gynostemium in the Disinae and Satyriinae.

The *Huttonaea*/*Brownleea*/Coryciinae-clade shows a development from the probably primitive entire stigma to two separate stigmas on the rostellum with generally flat to convex receptive area(s). In *Huttonaea*, the stigma is an entire convex cushion and also develops from a solitary structure (Kurzweil, 1989). In most *Brownleea* species, the stigma appears to be entire as well but is shallowly grooved in the middle by the adpressed lip. It was found to develop from two separate primordia next to each other (Linder & Kurzweil, in prep.). In some *Disperis* species, the appearance of the mature stigma is very similar to that of *Brownleea* (Kurzweil & Linder, 1991). In the remainder of *Disperis* two almost or completely separate stigmas are present. The Coryciinae sensu stricto, with their wide rostellums, have two separate stigmas throughout the ontogeny (Kurzweil, 1991; Kurzweil et al., 1991).

VII. POLLEN SURFACE

The surface topology and wall anatomy of the pollen surface (Figs. 24–32) provide a substantial set of data, which appear to have great phylogenetic value in the Orchidaceae (Burns-Balogh, 1983; Burns-Balogh & Funk, 1986). The palynology of the group has been studied by Schill & Pfeiffer (1977), Linder (1986), Chesselet (1989), and Chesselet & Linder (1993). The pollen is aggregated into sectile pollinia, which is typical of the subfamily (Lindley, 1830–1840; Burns-Balogh & Funk, 1986). The tetrads are combined into massulae, and the massulae are united into the pollinium. The massulae are easily separated, and the pollinium does not form a solid body.

The massulae vary extensively in shape. Some

of this variation may be related to the shape of the flower and the locules, but some appears to be phylogenetically interesting. Chesselet & Linder (1993) suggest that the massulae are rounded in most of the Disinae, while they are fasciculate in the Coryciinae sensu stricto. Rounded massulae were also observed in the few outgroup taxa studied, and may be the general condition in the Orchidoideae. This variation is largely correlated with the organization of the tetrads. The tetrads are generally tetrahedral in taxa with rounded massulae (Fig. 24), while linear tetrads are found in taxa with fasciculate massulae (Figs. 25, 28). However, while massula shape is easily determined, and relatively constant within samples and genera, the tetrad organization is more difficult to observe and appears to have exceptions. In no pollinia studied was the tetrad organization totally constant, but the frequency of tetrahedral and linear tetrads varied. There are exceptions to the simple pattern described above. *Corycium nigrescens* Sond., *C. dracomontanum* Parkman & Schelpe, and about half of the *Disperis* species do not have linear tetrads. The two *Corycium* species were ignored when the genus was coded for cladistic analysis. However, because about half of the *Disperis* species appear to have the primitive condition, *Disperis* has been coded for tetrahedral tetrads and nonfasciculate pollinia. A further problem with the character is that tetrad organization has not been widely studied in the subfamily. It is possible that tetrad organization actually causes the massula shape. There is scope for a more detailed, and possibly ontogenetic, investigation of this problem.

The wall structure has some commonalities across the tribe. A foot-layer is always absent, as is typical of the subfamily (Burns-Balogh, 1983). The columellae are always well developed. The wall is semitectate in most of the genera, but the wall is intectate in *Disa* sect. *Micranthae*, and it is secondarily tectate in the Coryciinae sensu stricto (*Corycium*, *Ceratandra*, *Evotella*, and *Pterygodium*). Although Burns-Balogh (1983) suggested that the Orchidoideae are primitively intectate, Chesselet & Linder (1993) propose that the semitectate condition is primitive in the Diseae. This is corroborated by the analyses here.

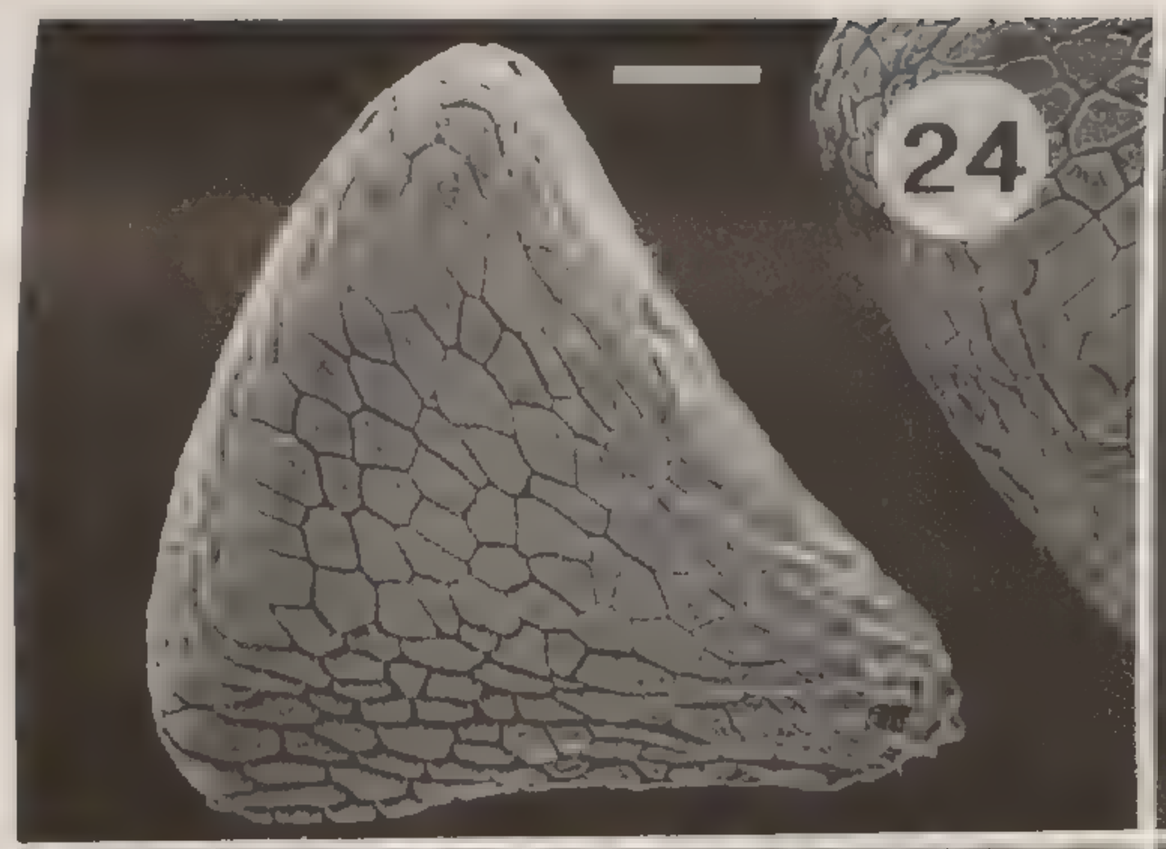
Pollen-surface ornamentation provides a wealth of useful data. The surface ornamentation is baculate in *Disa* sect. *Micranthae*, but is actually produced by the columellae, and is therefore not homologous with an ornamentation produced by the tectum. The walls are tectate in the Coryciinae sensu stricto, and the ornamentation consists of striations on the tectum. The remainder of the Diseae have semi-tectate walls which are either reticulate (Fig. 29) or have a more or less rugose or hamulate ornamentation (Figs. 30, 31). The Disinae generally have a rugose or hamulate ornamentation (Fig. 27). The situation in *Satyrium* is still confused, with an initial wide survey revealing extensive variation ranging from reticulate to hamulate ornamentation (Fig. 32). Hamulate ornamentation has also been recorded in two species of *Corycium* (*C. dracomontana* and *C. nigrescens*), while the rest of the Coryciinae have reticulate ornamentation. This suggests that a reticulate ornamentation may be the primitive condition in the Diseae, and that the hamulate condition may be treated as a synapomorphy for the Disinae. As the occurrence of hamulate pollen ornamentation is rare outside the Disinae, its occurrence was ignored when the genera were coded for the cladistic analysis.

VIII. SEEDS

The seeds are very uniform in the Diseae (Figs. 33–44, Kurzweil et al., 1991; Kurzweil, 1993b), and apparently do not carry much taxonomically useful information. The seeds of the Diseae are almost always minute and of the same structure as in the related tribe Orchideae (Healey et al., 1980; Barthlott, 1976; Ziegler, 1981; Tohda, 1983; Wildhaber, 1972; unpublished data). The seeds are usually fusiform in general shape as in most other orchids, although cylindrical and globose seeds occur occasionally (Fig. 39). The seed-coat consists of dead cells with their outer periclinal walls concave and adpressed to the inner one. The

→

FIGURES 24–32. SEM micrographs of pollen ultrastructures. Scale bars: 50 μm in 24–26, 5 μm in 27–32. 24–26. Massulae.—24. *Disa pulchra* Sond., with tetrahedral tetrads.—25. *Pterygodium alatum* (Thunb.). Sw., with elongated tetrads.—26. *Satyrium erectum* Lindl. 27–32. Surface ornamentation.—27. *Disa pulchra* Sond.; note the hamulate ornamentation.—28. *Pterygodium catholicum* (L.) Sw.; note the fasciculate massulae and linear tetrads. 29. *Disperis capensis* Sw., with a reticulate tectum.—30. *Satyrium sphaerocarpum* Lindl., with a finely rugose surface.—31. *S. erectum* Lindl., with a rugose surface.—32. *S. striatum* Thunb., with a hamulate surface. Sources (HK = H. Kurzweil). 24: *HK 1253*, 25: *HK 949*, 26: *HK 1508*, 27: *HK 1253*, 28: *HK 1543*, 29: *HK 1503*, 30: *HK 1424*, 31: *HK 1508*, 32: *HK 1369*.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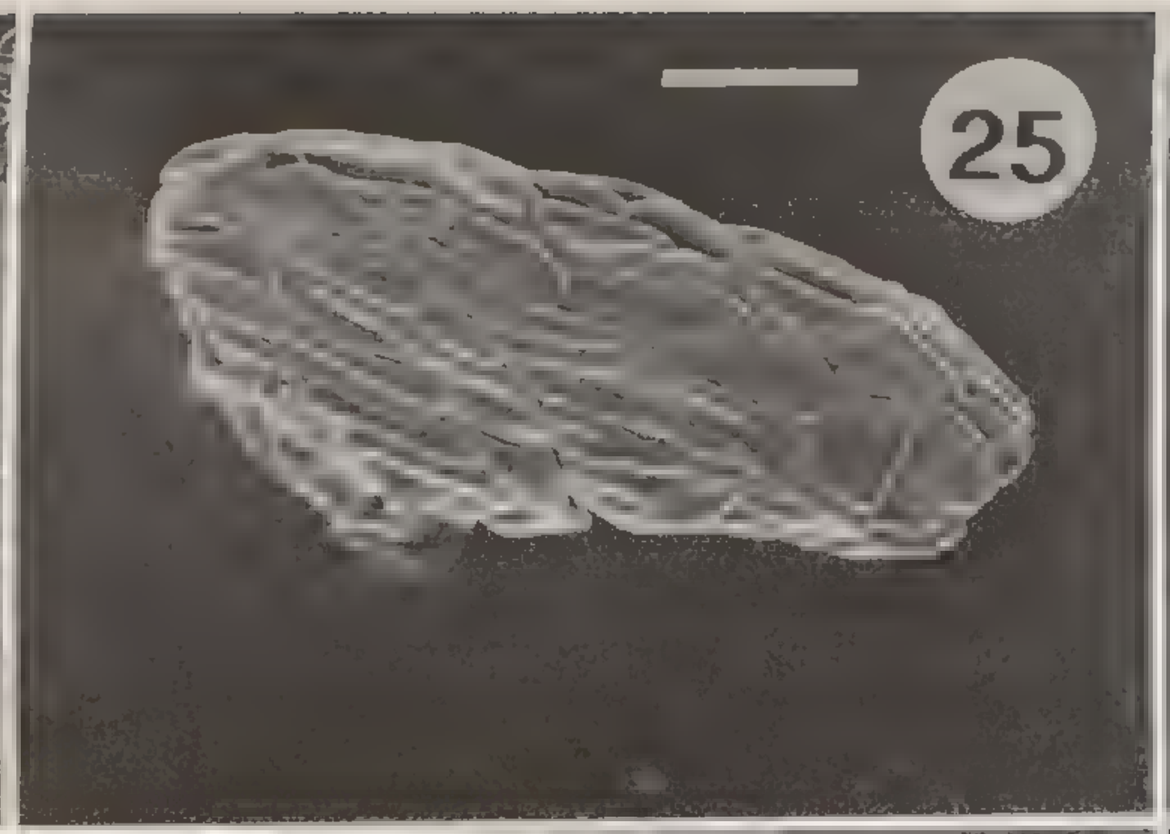
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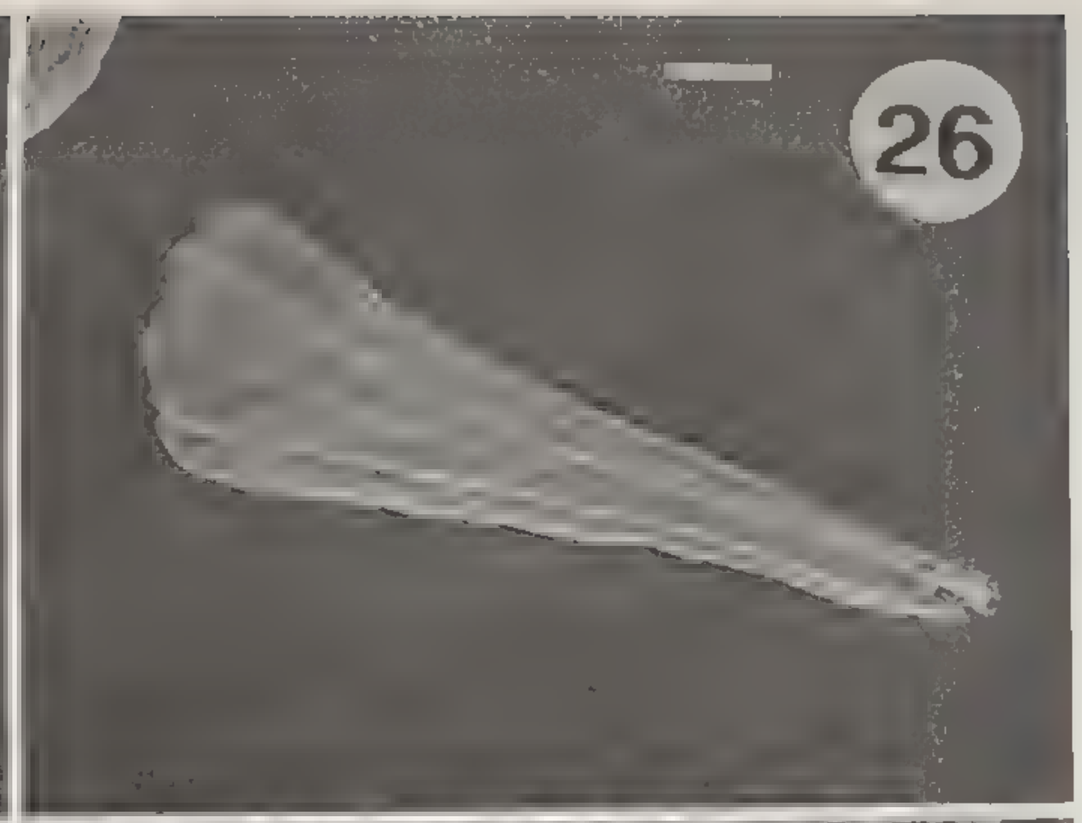
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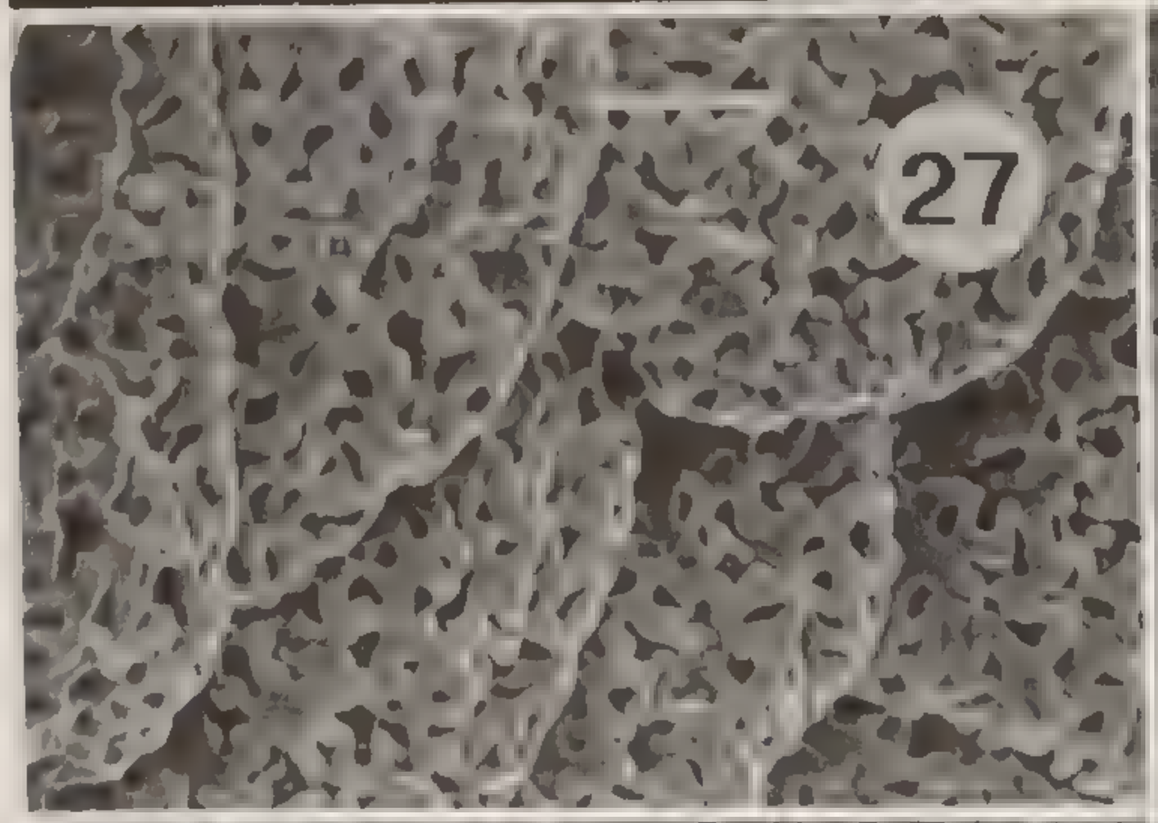
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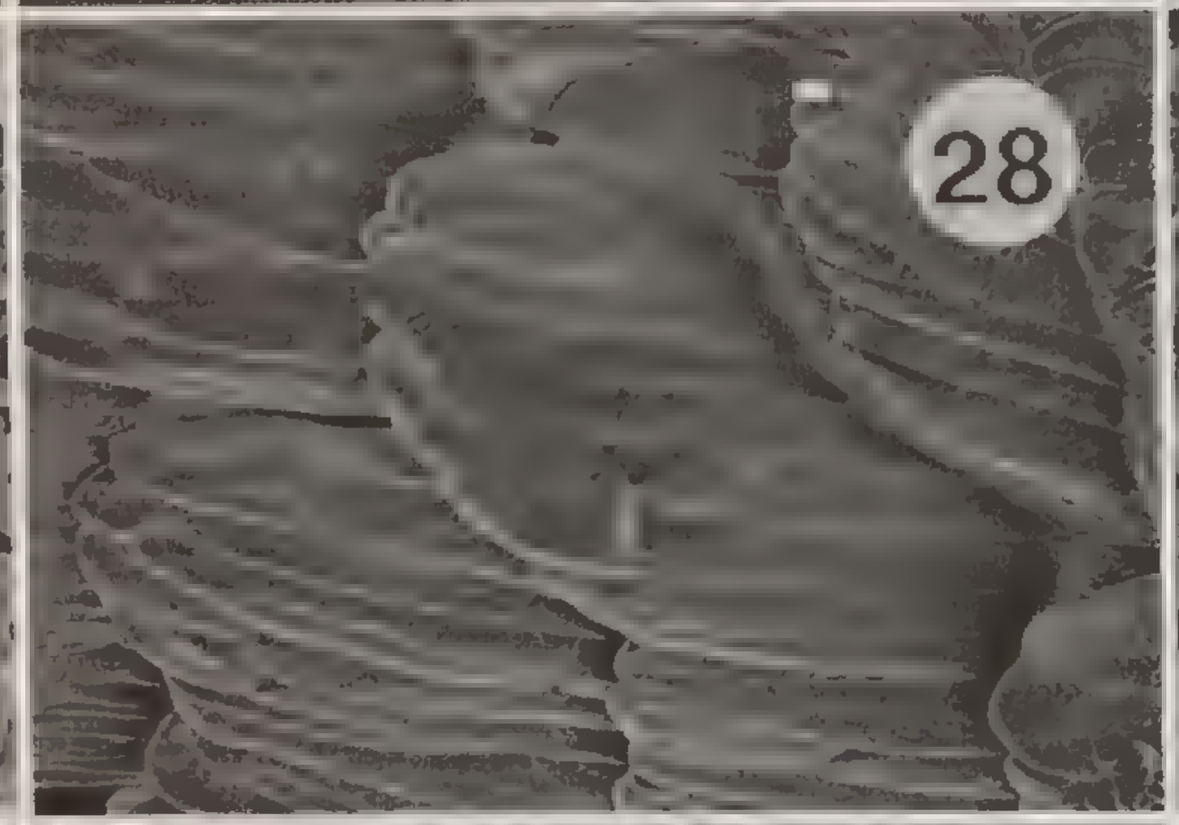
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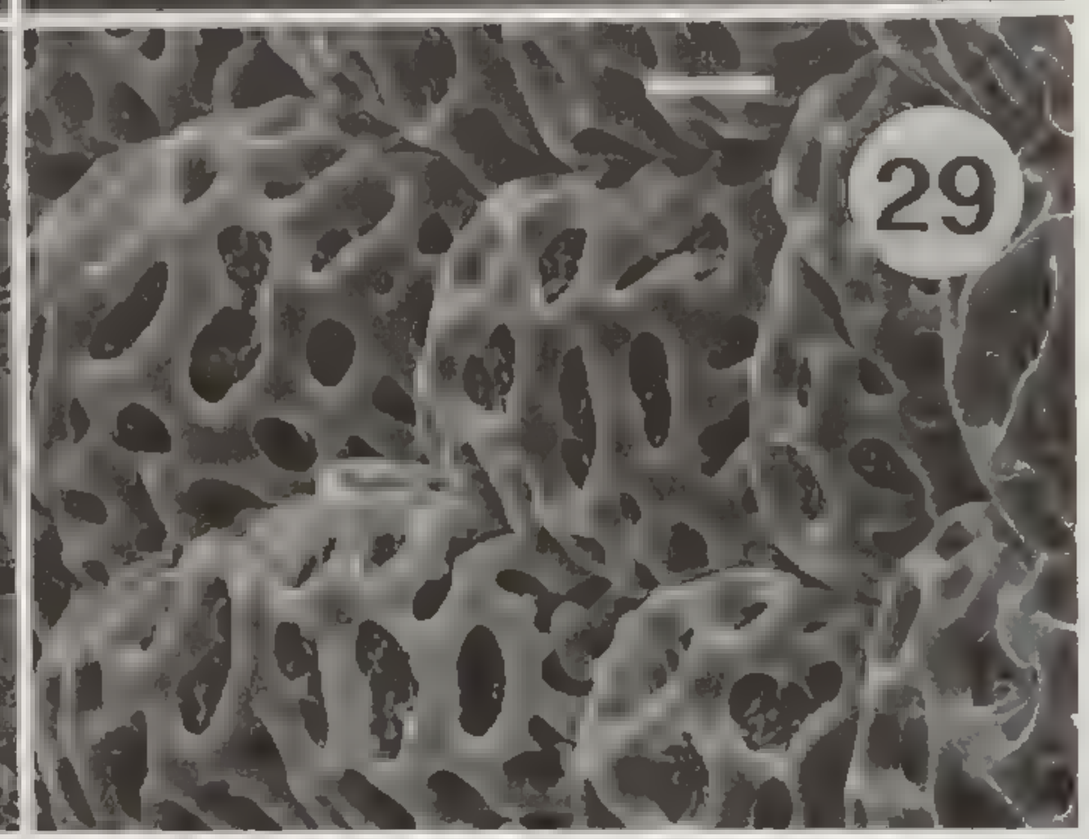
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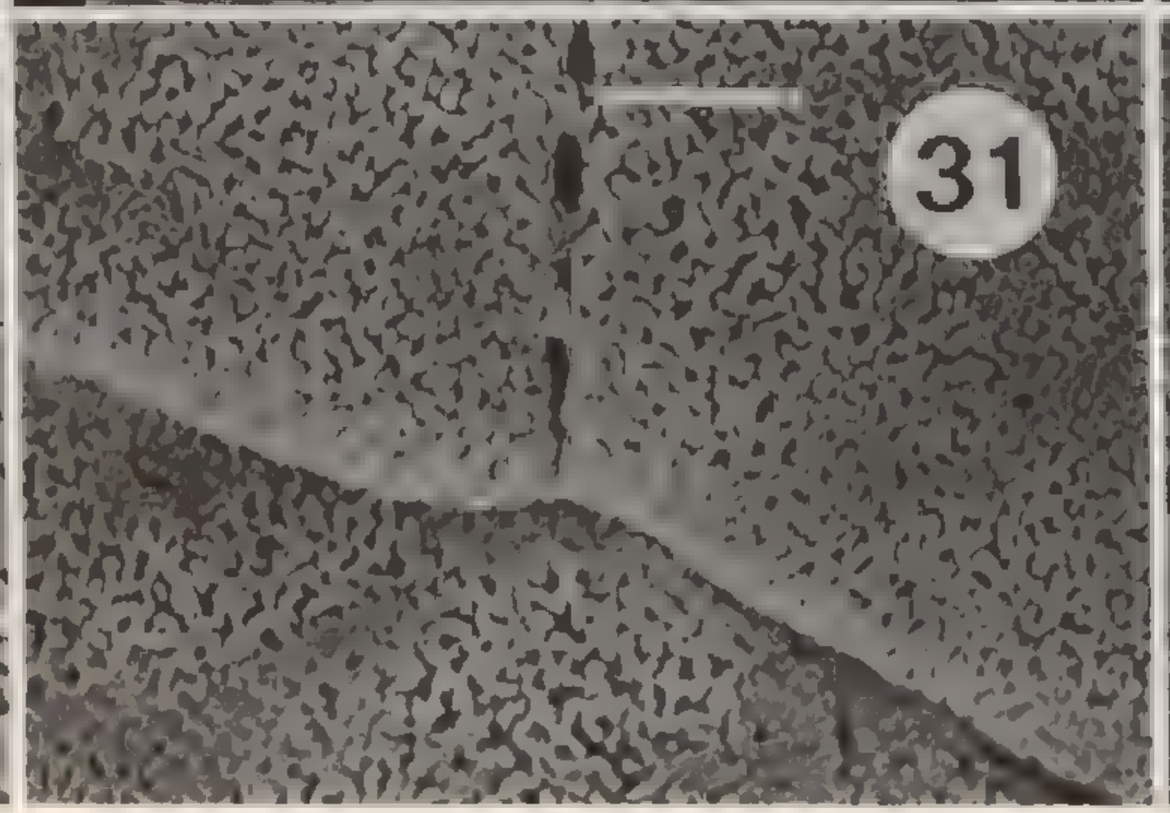
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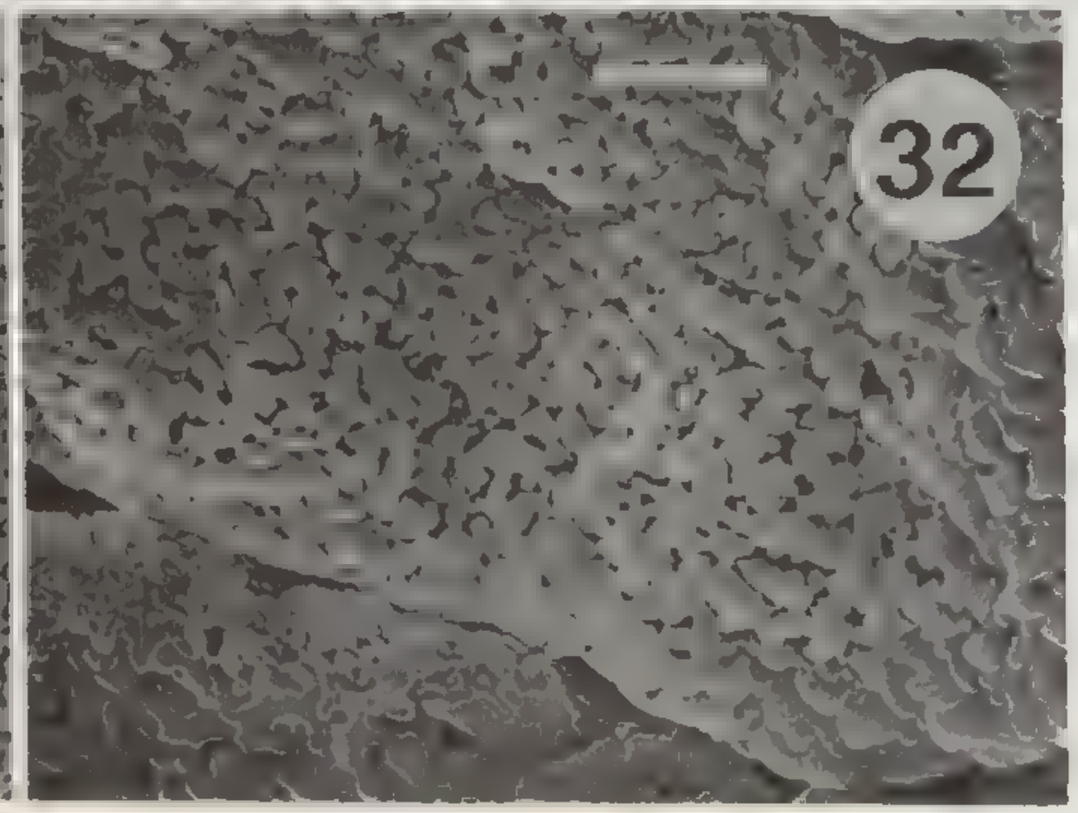
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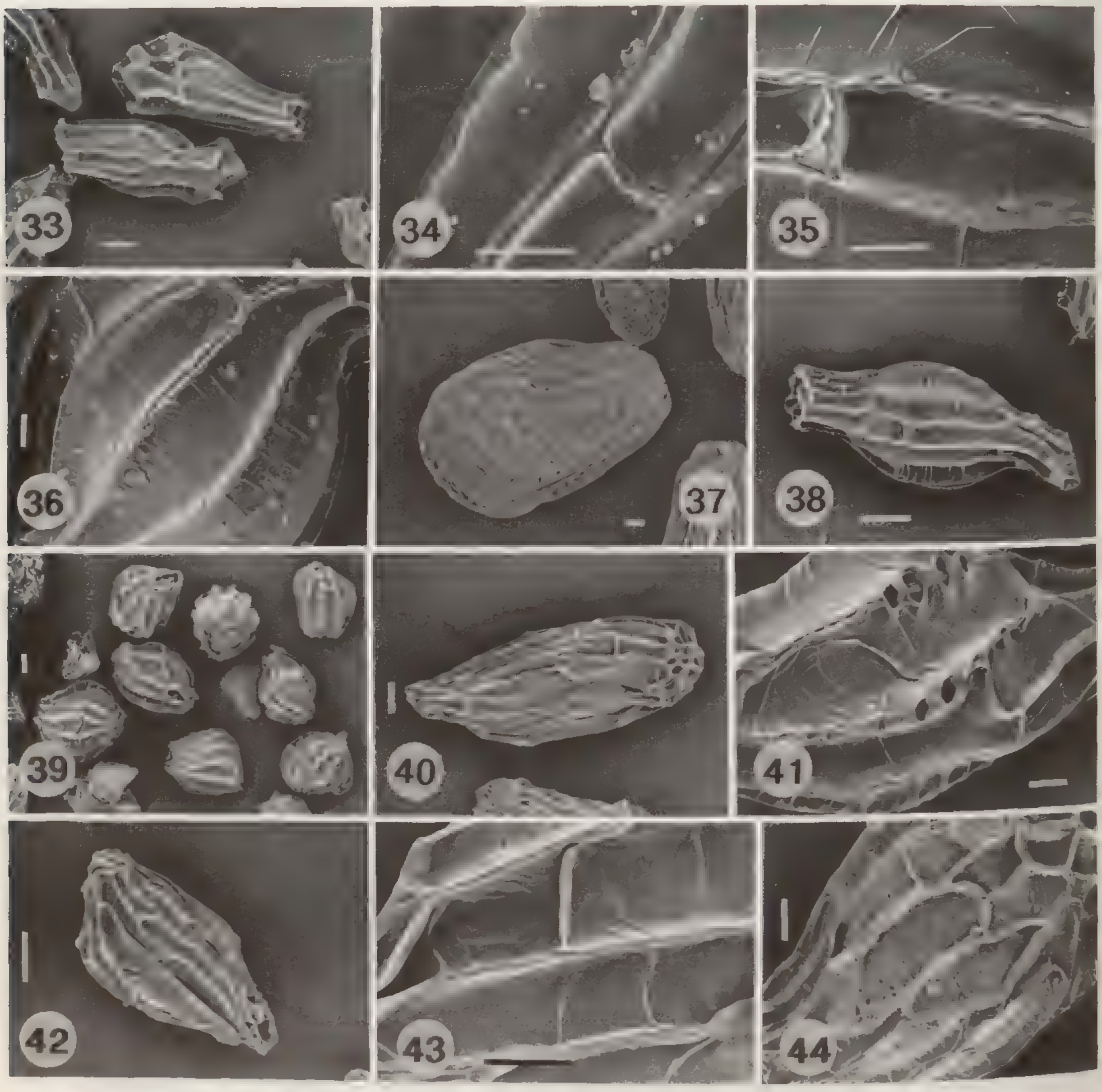

FIGURES 33–44. SEM micrographs of seeds and seed surfaces. Scale bars: 50 μm in 33, 37–40, 42; 20 μm in 34–36, 41, 43, 44. —33, 34. *Disa chrysostachya* Sw., with almost cylindrical seed and irregularly thickened anticlinal walls. —35. *D. caffra* H. Bolus; note the concavities in the marginal part of the periclinal walls. —36. *D. cornuta* (L.) Sw., with irregularly thickened walls. —37. *D. tripetaloides* (L.f.) N.E. Br.; note the large swollen seed. —38. *Monadenia bracteata* (Sw.) T. Durand and Schinz, with a typical fusiform seed. —39. *M. comosa* Rchb. f., with a globose seed. —40. *Brownleea macroceras* Sond., fusiform seed with comparatively thick anticlinal walls. —41. *Disperis renibractea* Schltr.; note the prominent holes between the anticlinal walls of adjacent cells. —42, 43. *Satyrium stenopetalum* Lindl. subsp. *stenopetalum*. —44. *Pachites bodkinii* H. Bolus, showing finely sculptured periclinal walls. Sources. 33, 34: *Levyns 10827*, 35: *McLoughlin 521*, 36: *Linder 3070*, 37: *Compton 12809*, 38: *Kurzweil 1384*, 39: *Fourcade 5064*, 40: *Bockelmann s.n.*, 41: *Schelpe 5258*, 42, 43: *Schelpe 5794*, 44: *Vlok 62*.

cells in the median portion of the seed are elongate, considerably larger, and also more regular in shape than the cells at both ends of the seed. The anticlinal walls are raised and are fused to the anticlinal wall of the adjacent cell. The fusion is usually not complete, and a groove indicates the derivation of the resulting "ridge" from two different anticlinal walls (especially at the corners of the cells). Prominent holes are visible between the anticlinal walls of adjacent cells (Fig. 41) in the *Disperis* species studied. The anticlinal walls may be somewhat enlarged and slightly projecting from the seed surface, but prominent hooks as in many vandoid orchids (Chase & Pippen, 1988) were not observed. They may also be variously irregularly thickened ("beaded" sensu Clifford & Smith, 1969). The anticlinal walls are straight or slightly wavy in the majority of species, but seeds with strongly undulating an-

TABLE 3. Character list for the Diseae. All multistate characters were coded as nonadditive characters.

1. Cauline leaves: all same size (0), grading from large at the base to small at the apex (1).
2. Sepals brightly colored (0), green (1).
3. Sepals often apiculate (0), almost never (1).
4. Dorsal sepal similar to the lateral sepals (0), dorsal sepals galeate (1).
5. Dorsal sepal ecalcarate (0), spurred (1).
6. Petals similar to the lateral sepals (0), different (1).
7. Petals fused to gynostemium (0), free (1).
8. Petals adnate to dorsal sepal (0), free (1).
9. Strongly developed petal nerves absent (0), petal nerves frequently present (1).
10. Lip fused to base of gynostemium (0), free (1).
11. Lip with a fundamentally bilobed appendage (0), not (1).
12. Lip with two spurs (0), unspurred (1), with one spur (2).
13. Lip galeate (0), not (1).
14. Lip erect at the base (0), patent or descending at the base (1).
15. Lip appendage bilobed (0), single and fused (1).
16. Lip blade simple (0), spathulate and anchor-shaped (1).
17. Column-part well developed (0), not and very short (1).
18. Lateral gynostemium appendages well developed (0), small to absent (1).
19. Anther erect (0), reflexed (1).
20. Anther cells adjacent (0), widely separated by a wide connective (1).
21. Pollen tetrads tetrahedral (0), elongated (1).
22. Massulae rounded (0), massulae fasciculate (1).
23. Pollen surface sculpturing reticulate (0), rugose or hamulate (1), striate (2).
24. Pollen surface semi-tectate (0), secondarily tectate (1).
25. Rostellum three-lobed (0), only the central lobe developed (1).
26. Rostellum central lobe an intrathecal tooth (0), reduced or small to lost (1), flat and covering both theca (2), massive and making up the whole rostellum (3), massive between small lateral rostellum lobes (4).
27. Rostellum lateral lobes square to elongate-erect (0), minute (1), elongate-spreading (2).
28. Rostellum with elongated spreading lateral lobes which are flat and expanded (0), projecting (1), twisted (2).
29. Stigma sessile on the gynostemium (0), subterminal (1).
30. Stigma produced from all three carpels (0), median only (1).
31. Median carpel stigmatic part from one primordium (0), two primordia (1).

ticlinal walls were found in *Ceratandra*, *Corycium carnosum* (Lindl.) Rolfe (Kurzweil et al., 1991), and in *Satyrium retusum* Lindl. (Kurzweil, 1993b). The surface of the periclinal cells is variously smooth to more or less wavy; however, the prominent ornamentation found in several Orchideae (Barthlott, 1976; Healey et al., 1980; Tohda, 1983) was not observed here. The marginal parts of the periclinal cells have occasionally small shallow concavities (Fig. 35, observed in five species). Periclinal ridges are well developed as in the Orchideae, but their intervals as well as their thickness and number are too variable to give any phylogenetic information.

A remarkably different seed type was found in *Disa tripetaloides* (L.f.) N.E. Br., *D. uniflora*, *D. cardinalis* Linder, and *D. caulescens* Lindl., which have considerably larger seeds and numerous surface cells with slightly convex periclinal walls (Fig. 37, Kurzweil, 1993b).

CLADISTIC ANALYSIS

The characters that were found to be cladistically informative are listed in Table 3, and their distribution among the taxa is given in Table 4.

The cladistic analysis located three trees with a length of 57 steps, a consistency index of 66, and a retention index of 85. Two of the three trees show different topologies for the basal node of the Diseae (Fig. 45A, B), while the third tree is a more resolved topology of the second tree, and the consensus tree shows a basal polychotomy for the subtribes (Fig. 45C). The successive weighting had to be run twice before the cladogram stabilized. Two trees were located, which differed only in the arrangement of the three outgroup taxa. This is the basic topology presented in Figures 46 and 47, on which the subsequent discussion is based. The supporting characters for the cladogram are given in Figure 46, and the node numbers and "bootstrap percentiles" are indicated in Figure 47.

SYSTEMATIC INTERPRETATION

DISEAE

Dressler's (1981) concept of a single tribe, the Diseae, to combine the groups with reflexed anthers, is supported (contrary to Szlachetko, 1991), and this group is retrieved at node 13. This node is supported by a single character (reflexed anther, character 19) which reverses for one group (*Disa* sect. *Micranthae*). Dressler (1981) also based his recognition of the Diseae on this character, and Burns-Balogh & Funk (1986) noted that the Disinae and Satyriinae both have bent gynostemium apices, which may refer to the same condition. The node has a "bootstrap percentile" of 62, but this analysis does not present a rigorous testing of the hypothesis of monophyly for the Diseae, as only

TABLE 4. Distribution of characters among the taxa. *Disa* refers to the genus *Disa* excluding section *Micranthae*, while *Micranthae* refers to *Disa* sect. *Micranthae*. Missing or variable characters, or logically inapplicable characters are coded as "?."

Brachycorythis	11100	10111	12100	01000	00000	00?00	0
Holothrix	11100	11101	12100	01100	00000	00?00	0
Schizochilus	11100	11101	12100	01000	00000	00?00	0
Satyrium	10100	011?1	10000	00?10	00000	?1?10	0
Pachites bodkinii	10100	01111	11100	00010	00000	10?10	0
Pachites adpressa	10100	01111	11100	00?10	00000	41?10	0
Satyridium	10100	01111	10000	00110	00001	3??10	0
Disa	10011	10101	11110	01010	00100	00?10	0
Herschelianthe	10011	10101	11110	01010	00100	00?10	0
Micranthae	10011	10101	11110	01000	00100	00?10	0
Monadenia	10011	10101	11110	01010	00101	31?10	0
Schizodium	10011	10101	11100	01010	00100	00?10	0
Brownleea	10111	10010	11100	01010	00000	10?01	1
Huttonaea	11100	11101	11110	01010	10000	41?01	0
Disperis	1?1??	11010	01100	01010	00000	22101	1
Corycium	11100	11010	01101	01111	11210	12201	1
Ceratandra	01100	11010	01100	11111	11210	12001	1
Evotella	01100	11010	01100	11111	11210	12001	1
Pterygodium	11100	11010	01101	01111	11210	12201	1

three genera of the Orchideae were used in the outgroup. One of these genera, *Brachycorythis*, has several characters in common with some members of the Diseae, and this probably accounts for the relatively low "bootstrap percentile" for this node. It would be necessary to analyze the whole subfamily Orchidoideae in order to substantiate the monophyly of the Diseae—such a global analysis is long overdue.

Two clades are recognized in the Diseae. The first clade (node 10) includes the Satyriinae and the Disinae, excluding *Brownleea*. The second clade (node 12) includes the Coryciinae, as well as *Huttonaea* and *Brownleea*.

In two of the three fundamental trees, the Satyriinae are combined with the Disinae at node 10 (Fig. 46). The characters supporting this arrangement are the subterminal stigma (character 29) and the brightly colored sepals (character 2). The former character was also used by Bentham & Hooker (1883) and Pfitzer (1889) to diagnose this group, while Rolfe (1912–1913) separated his Diseae from the Corycieae by the lip not being fused to the gynostemium (thus implying that the Diseae sensu Rolfe is paraphyletic, as the Diseae are then based on the absence of a character). Neither character is very good. A subterminal stigma is difficult to define clearly and may also occur in the Coryciinae, where the floral structure is too contorted to make such fine distinctions. Brightly colored sepals also occur sporadically in other groups. Schlechter (1901), who also recognized this group, criticized the characters used by Bentham & Hooker (1883) and Pfitzer (1889), and suggested that a raised and sharply delineated stigma, as well as a tall rostellum, may better define the group. However, both these characters occur in modified form in the Coryciinae. It is therefore evident that, although the group has been frequently recognized in the past, it lacks convincing empirical support. The "bootstrap percentile" for this node is only 13, thus indicating that there is little support for the combination of the Disinae and the Satyriinae, as suggested by Bentham & Hooker (1883), Pfitzer (1889), Schlechter (1901), and Rolfe (1912–1913).

This very low percentile may be affected by the interpretation of the evolutionary origin of *Brownleea*. *Brownleea* is placed in the Coryciinae clade in the tree located by successive weighting, as compared to its previous position in the Disinae. An inspection of the character distributions shows that it has many of the characteristic features of both the Disinae and the Coryciinae. These may have evolved in parallel in *Brownleea* and the Disinae, as a result of a similar pollination syndrome, compared with the oil-collecting bee syndrome that appears to be central to the evolution of the coryciinoid flower structure. This might account for the spurred dorsal sepal and the brightly colored tepals, with the fusion between the petals and the gynostemium providing mechanical strength for directing the pollinator into the spur of the dorsal sepal.

An alternative hypothesis could be that *Brownleea* originated as a hybrid between the Coryciinae and the Disinae. The cladistic results were inves-

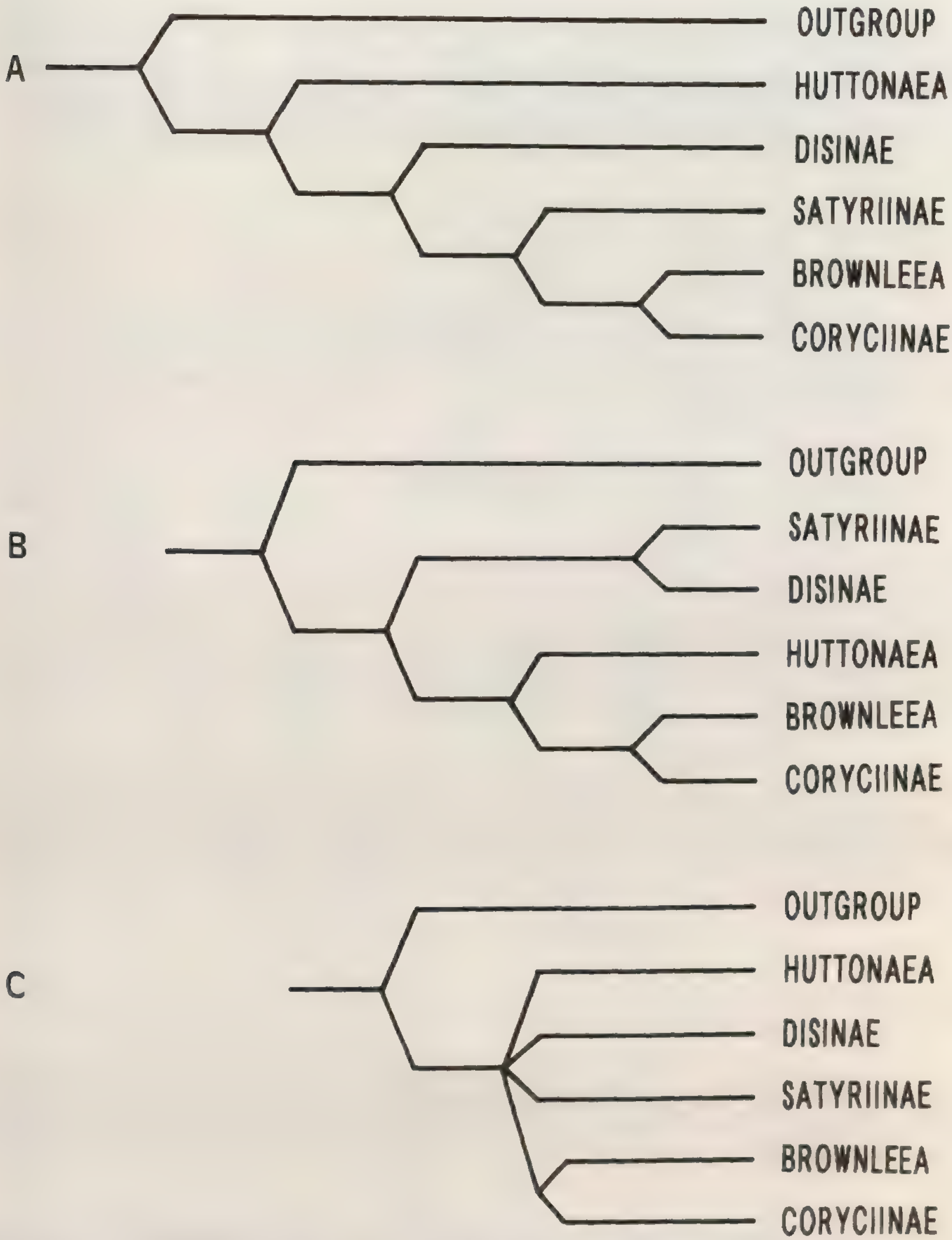

FIGURE 45. The basic structure of the trees retrieved in the analysis.—A. Fundamental tree 1.—B. Fundamental tree 2.—C. Strict consensus tree of the three fundamental trees. The outgroup is as defined in the text.

tigated for patterns that might corroborate such a hybrid origin. Funk (1985a) suggested seven criteria by which hybrids can be recognized cladistically.

(1) "When there are two cladograms of similar length and one taxon position changes, the taxon that is moving may be a hybrid and the two taxa between which it is moving may be the parents." This pattern was not observed in this study. In the three equal length trees the components below the

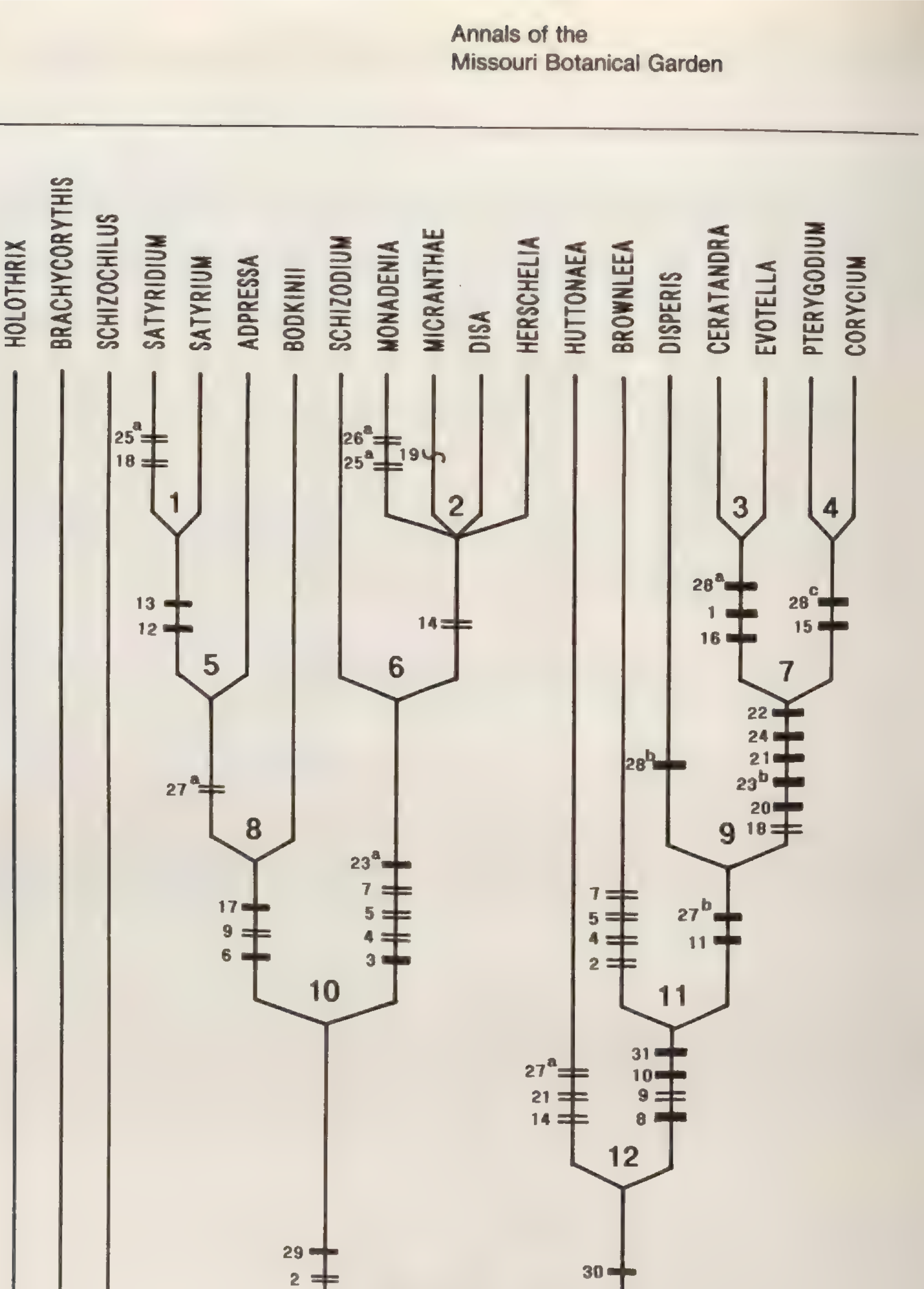

FIGURE 46. One of the two shortest cladograms of the tribe, showing the distribution of the characters numbered according to Table 2. Solid bars indicate unique synapomorphies; parallel lines indicate characters that evolved several times and wavy lines indicate reversals. The larger numbers at the nodes indicate the node numbers referred to in the text.

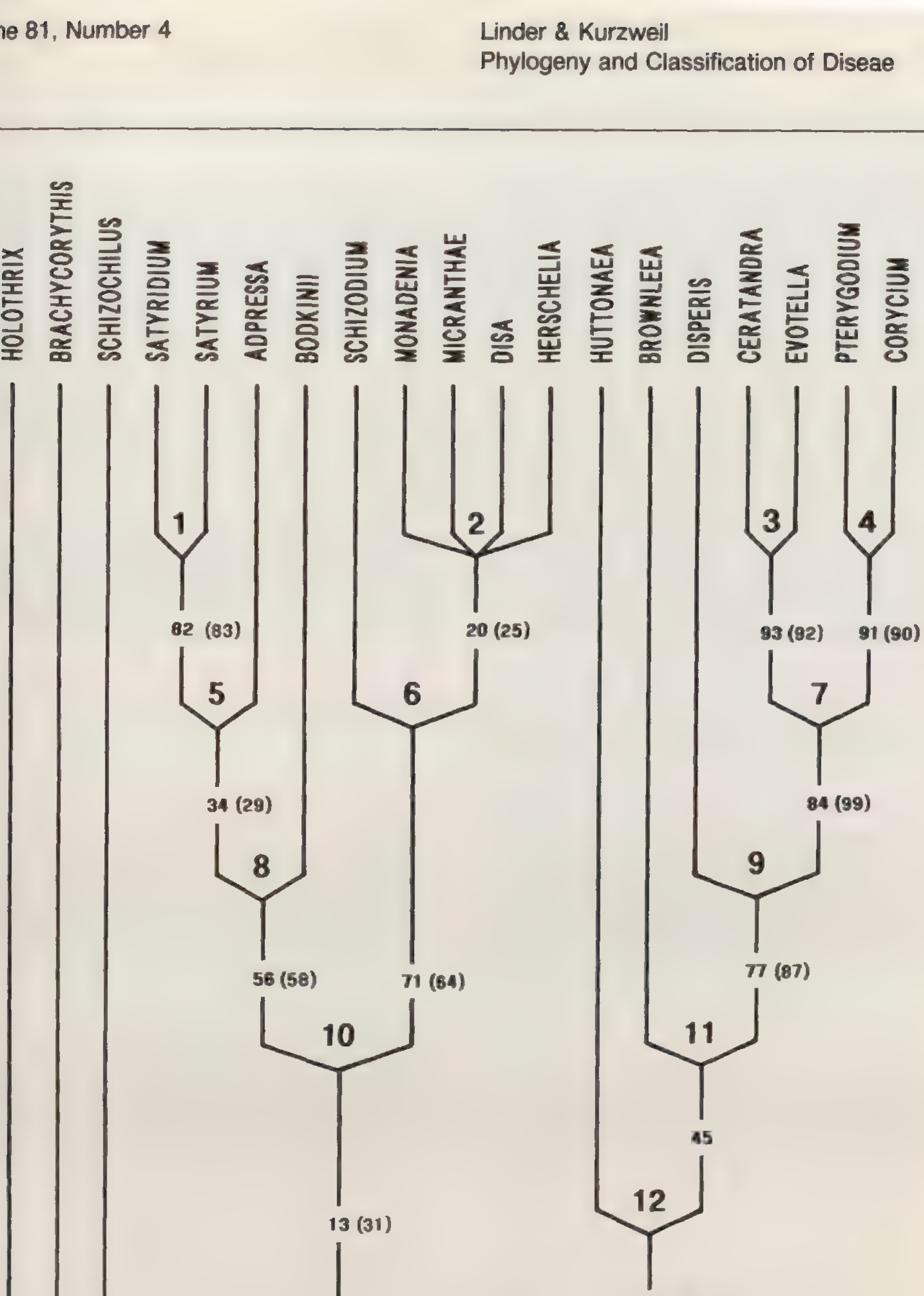

FIGURE 47. Cladogram given in Figure 46, with the bootstrap confidence percentiles indicated at each node, and the percentiles calculated with *Brownleea* excluded from the analysis given in brackets. The nodes are numbered as in Figure 46.

hybrid are variously arranged; but *Brownleea* is always associated with the Coryciinae.

(2) ". . . it is possible to follow a path of character conflicts." Thus there should be a set of character conflicts, showing that the hybrid contains the synapomorphies of the two parental lineages. This is evident in this case, as *Brownleea* has virtually all autapomorphies of the Coryciinae as well as those of the Disinae. The coryciinoid characters are the petals adnate to the dorsal sepal (8), a lip that is fused to the gynostemium (10), a stigma produced only from the median carpel (but see the discussion of this character above) (30), as well as the stigmatic part of the median carpel developing from two primordia (31). The disinoid characters are the galeate and spurred dorsal sepal (4, 5) and the petals which are fused to the gynostemium (7). By moving *Brownleea* from one clade to the other, the clade without *Brownleea* is virtually rendered paraphyletic, which it would of course be if *Brownleea* is of hybrid origin.

(3) "Taxa that are defined solely by character conflicts may be hybrids or parents." This applies, in the tree in Figure 46, to the Disinae, which are here postulated as one parent. If *Brownleea* were to be included in the Disinae, the Coryciinae would be defined by seven characters, of which five are conflicting. This would identify the Coryciinae as the other parent.

(4) "Taxa with reversals may be hybrids." *Brownleea* shows no reversals.

(5) "Taxa without autapomorphies may be parents." This is effectively the same as (3).

(6, 7) The lack of consensus on a strict consensus tree may be traced to a hybrid taxon. This is indeed what is found here; with three equal length trees the consensus gives a basal polychotomy (Fig. 45C). To test whether *Brownleea* is causing the collapse of the cladogram, this taxon was removed from the data-matrix. The analysis without *Brownleea* produced a single most parsimonious tree, identical to the tree retrieved by successive weighting (Figs. 46, 47), with a consistency index of 73 (compared to 67 for the analysis including *Brownleea*), thus clearly demonstrating that the problem lies with *Brownleea*.

A further criterion for hybrid recognition can be introduced. If the hybrid is removed from the data-matrix, and a bootstrap analysis is re-run, the nodes below the parents of the hybrid should have a higher percentile support. This was found here, with the nodes below the Disinae increasing from 13% to 31%, and below *Huttonaea* from 17% to 45% (Fig. 47).

Phipps et al. (1991) in an analysis of the Maloideae (Rosaceae), which are also of putative hybrid origin, suggest that complex character incongruence within the maloids might have been the result of polychotomous early evolution within the clade, caused by the hybrid origin. Within *Brownleea* there are also reversals in quite "fundamental" characters and unusual character combinations (Linder & Kurzweil, in prep.), which might also indicate early polychotomous evolution caused by a hybrid origin.

Although hybrid species have frequently been demonstrated cladistically (Funk, 1982, 1985a; Humphries, 1981; Wagner et al., 1985), there have been relatively few such demonstrations at higher taxonomic levels (e.g., the Maloideae, Phipps et al., 1991).

SATYRIINAE

The Satyriinae, including *Pachites*, *Satyridium*, and *Satyrium*, form a rather weakly supported group, with only three synapomorphies and a "bootstrap percentile" of 56 (see Fig. 47, node 8). The most important character combining the taxa in this group is the elongated column-part, which is unique in the Orchidoideae (character 17). A second synapomorphy for this group is the lack of differentiation between the petals and the sepals, but this may well be a plesiomorphic condition, as it is the ancestral orchidaceous condition. Dressler (1981) suggested that the lack of resupination may also be used as a character, but this recurs frequently in the Diseae and cannot be given much emphasis. The two species of *Pachites* do not group together, indicating that they do not form a monophyletic group, and that the genus should be subdivided. Although the two species share the same general appearance, this is largely due to symplesiomorphic characters, and they have very different gynostemium structures. Both species of *Pachites* are lacking in derived features, making their placement anywhere complicated, and lowering the "bootstrap percentiles" linking them in anywhere. As the one peculiar feature they share is the elongated column-part, they are probably best kept in the Satyriinae.

DISINAE

The Disinae, even with the removal of *Brownleea*, form a moderately supported group, as indicated by node 6 (Fig. 47). This node is supported by two unique characters, and by three characters shared with *Brownleea*, and has a "bootstrap per-

centile" of 71. Neither of the two unique synapomorphies for the group is very convincing. Character 3, the presence of apiculate sepals, may be the retention of an ancient monocotyledonous character that occurs widespread in the subclass (see Weber, 1980). Character 23, a rugose or hamulate pollen surface, also occurs sporadically in other groups in the Orchidoideae. The other characters (4, 5, 7) are linked to a pollination system shared with *Brownleea*: brightly colored sepals, a spurred dorsal sepal, and the petals fused to the base of the gynostemium. With *Brownleea* included, the subtribe would be much better supported—this is discussed above. The included taxa show a great deal of phenetic similarity, thus bedeviling the generic classification, and confounding any attempt up until now to delimit monophyletic genera in it. In addition, *Disa* is most probably not monophyletic. This is indicated by the lack of resolution within the clade.

CORYCIINAE

The Coryciinae form a clearly monophyletic group, but the critical issue is the delimitation of the subtribe. The Coryciinae sensu stricto (Kurzweil et al., 1991), including the genera *Evotella*, *Ceratandra*, *Corycium*, and *Pterygodium* (Fig. 47, node 7) are very well supported by five unique synapomorphies and one parallel character, and consequently it is not surprising that it has a "bootstrap percentile" of 84. If *Disperis* is included (the classical delimitation of the Coryciinae, followed by all previous authors), then only two characters are synapomorphic for the group, but the "bootstrap percentile" is still relatively high at 77. This lower level of support suggests that the Coryciinae could be delimited excluding *Disperis*. If *Disperis* were to be excluded from the Coryciinae, it would have to be placed in its own subtribe. However, a subtribe containing a single genus does not carry any information, and the information that *Disperis* is the sister taxon to the Coryciinae sensu stricto can be presented by the sequencing conventions of Wiley (1981). On balance, it would appear to be more informative to include *Disperis* in the Coryciinae.

BROWNLEEA

The phylogenetic position of *Brownleea* could be indicated by sequencing criteria, thus obviating the need for a special subtribe for the genus. However, from the bootstrap analysis it is evident that there is rather ambiguous support for a clade including *Brownleea* and the Coryciinae, and therefore this would be a poor node at which to establish a formal taxon (Linder, 1991), as further information may result in a change in that portion of the cladogram. Formal taxa should be established at nodes with a high "bootstrap percentile," because these are more robust, and thus less sensitive to new data.

In addition, as was argued above, there is a strong possibility that *Brownleea* may have originated as a hybrid between the Coryciinae and the Disinae. If *Brownleea* were of hybrid origin, then *Brownleea* plus the Coryciinae would not be a monophyletic taxon, as it would include genetic material from two distinct ancestors. As monophyly is the single most important criterion for a taxon (Wiley, 1981; Funk, 1985b), this would argue strongly against including *Brownleea* in the Coryciinae. Hybrid taxa are polyphyletic, and the best approach may be to define them as narrowly as possible, and to give them the same rank as their parents.

Placing *Brownleea* in a distinct subtribe from the Coryciinae would emphasize the very real differences between the two groups. With *Brownleea* excluded, the Coryciinae form a relatively uniform taxon, with a relatively uniform pollination syndrome, and may similar structures. The group is biologically homogenous. With *Brownleea* included, the group becomes biologically more diverse, and predictions or general biological statements about the group are greatly reduced. Classifications should be "maximally informative" (Wiley, 1981) or as Stevens (1985) noted, limits of genera (or all taxa) can be adjusted to serve many purposes, including that they be separated by a clear morphological gap.

We therefore argue that because the "bootstrap percentile" is relatively low, *Brownleea* is biologically rather different from the Coryciinae, and the possibility that it may be of hybrid origin cannot be discounted; it would be most informative to place it in its own subtribe.

HUTTONAEA

If *Brownleea* is placed in its own subtribe, then it follows that *Huttoneae* must also be recognized, at least at the subtribal level, in order to maintain the monophyly criterion.

However, the situation does change if the hypothesis that *Brownleea* is a hybrid could be corroborated. It would no longer be logically incorrect to include *Huttonaea* in the Coryciinae, because it would be the sister group to the Coryciinae as

presently circumscribed. There is little character support for including *Huttonaea* in the Coryciinae. Even with *Brownleea* excluded from the analysis, the "bootstrap percentile" is a low 45 and there is only a single character supporting the node. However, this character (a stigma derived solely from the median carpel apex) can be regarded as a "fundamental" character that is well understood both ontogenetically and in terms of its taxonomic distribution.

As with *Brownleea*, two arguments could be advanced against including *Huttonaea* in the Coryciinae. First, *Huttonaea* is morphologically very peculiar and has been placed in its own subtribe by both Senghas (1973–1974) and Dressler (1981). The pollination biology is not known, but the gynostemium shows little general resemblance to the Coryciinae, and the perianth is very different. This great degree of dissimilarity would be lost if they were to be included in the same subtribe. Second, the "bootstrap percentile" for the node, even with *Brownleea* excluded, is a low 45, reflecting the fact that at present a single synapomorphy is known for the group. This implies that the node would be very susceptible to new data. As *Huttonaea* is at present in its own subtribe, it would be conservative to retain this situation until more information is available, and more robust solutions can be found.

Formal Classification

Tribe ORCHIDEAE.

Lip usually spurred, anther erect. This tribe includes about 1700 species (Dressler, 1981).

Tribe DISEAE Dressler, Selbyana 5: 204. 1979.

Anther reflexed, lip spurless or with two spurs. Includes ca. 420 species, largely African with a few species reaching the Far East.

Subtribe SATYRIINAE Schlechter, Notizbl. Bot. Gart. Berlin-Dahlem 9: 568. 1926. Satyrieae (Schlechter) Szlach., Folia Geobot. Phytotax. 26: 326. 1991.

Petals similar to the lateral sepals, column-part elongated. Ca. 106 species.

Pachites Lindl., Gen. Sp. Orch.: 301. 1835.

This includes two species (Stewart et al., 1982), but as noted above the genus is probably not monophyletic.

Satyridium Lindl., Gen. Sp. Orch.: 345. 1838.

Monotypic (Linder, 1989).

Satyrium Swartz in Kong. Vet. Akad. Handk. 21: 214. 1800.

This genus has not yet been revised over its whole distribution range, and estimates of the number of species range from ca. 100 to 117 (Summerhayes, 1968; Hall, 1982; Linder, 1989).

Subtribe DISINAE Bentham, Gen. Pl. 3: 464. 1883.

Dorsal sepal spurred; petals adnate to the gynostemium; sepals apiculate; pollen surface rugose or hamulate. 168 species.

Schizodium Lindl., Gen. Sp. Orch.: 358. 1838.

Six species (Linder, 1981b).

Disa Bergius, Descrip. Pl. Cap.: 348. 1767.

128 species (Linder, 1981c, f).

Herschelianthe Rauschert, Feddes Repert. 94: 434. 1983.

The correct name of this genus is at present problematic. Rauschert (1983) suggested that the name it was originally known under, *Herschelia* Lindl., is a homonym for *Herschellia* Reichb.f., and proposed the new name *Herschelianthe*. The oldest name available is *Forficaria* Lindl. Either *Herschelia* Lindl. should be conserved, or *Forficaria* should be applied. As this group of "blue disas" are well known under *Herschelianthe*, we are using this name here, while recognizing that it is not nomenclaturally the correct name. 18 species (Linder, 1981e).

Monadenia Lindl., Gen. Sp. Orch.: 356. 1838.

16 species (Linder, 1981d).

Subtribe **BROWNLEEINAE** Linder & Kurzweil, subtribe nov. TYPE: *Brownleea* Harv. ex Lindl.

A Disinis labio erecto, petalis sepalo dorsali connatis, a Coryciinis petalis gynostemio connatis recedit.

Lip erect, reduced and fused to the base of the gynostemium; the petals adnate to the dorsal sepal and fused to the gynostemium.

Brownleea Harv. ex Lindl. in Hook. Lond. J. Bot. 1: 16. 1842.

Includes seven species (Linder, 1981a, 1985).

Subtribe HUTTONAEINAE Schlechter, Notizbl. Bot. Gart. Berlin-Dahlem 9: 568. 1926. Huttonaeae (Schlechter) Szlach., Folia Geobot. Phytotax. 26: 326. 1991.

Stigma derived only from the median carpel apex; anthers diverging; petals clawed and fimbriate.

Huttonaea Harv., Thes. Cap. 2: 1. 1863.

Five species (Stewart et al., 1982).

Subtribe CORYCIINAE Bentham, Gen. Pl. 3: 464. 1883. Corycieae (Bentham) Szlach., Folia Geobot. Phytotax. 26: 326. 1991. Disperidinae Schlechter, Bull. Herb. Boiss. 6: 800. 1898.

Stigma derived only from the median carpel apex; lip with an appendage and fused basally to the gynostemium. Ca. 134 species.

Disperis Swartz, Kongl. Vet. Akad. Handl. 21: 218. 1800.

This is a wide-ranging genus, reaching from southern Africa to New Guinea, and the precise number of species is not known. The current estimates are ca. 84 (Verdcourt, 1968; Manning, pers. comm.).

Ceratandra Ecklon ex Bauer, Ill. Orch. Plants 4 t. 16. 1827.

Six species (Kurzweil et al., 1991).

Evotella Kurzweil & Linder, Pl. Syst. Evol. 175: 215. 1991.

Monotypic.

Pterygodium Swartz, Kongl. Vet. Akad. Handl. 21: 217. 1800.

18 species (Kurzweil et al., 1991; Hunt, 1968).

Corycium Swartz, Kongl. Vet. Akad. Handl. 21: 220. 1800.

14 species (Kurzweil et al., 1991).

Key to the Genera in the Diseae

1a. Column-part elongated; petals and sepals rather similar (Satyriinae).
  2a. Lip with two spurs, these sometimes reduced to saccae or rarely lost; lip galeate or hood forming.
    3a. Viscidium solitary; stigma pulvinate ..... *Satyridium*
    3b. Viscidia usually paired; stigma flaplike ..... *Satyrium*
  2b. Lip scarcely different from the petals and never spurred.
    4a. Lip with small side lobes ..... *Pachites bodkinii*
    4b. Lip without small side lobes ..... *Pachites appressa*
1b. Column-part short or missing; petals and sepals generally quite different.
  5a. Petals spathulate; the margins deeply fimbriate; anther cells diverging (Huttonaeinae) ..... *Huttonaea*
  5b. Petals not spathulate, entire or lobed (Coryciinae and Brownleeinae).
    6a. Petals adnate to the dorsal sepal to form a galea; lip ascending at the base and appressed to the stigma.
      7a. Lateral sepals spurred or saccate ..... *Disperis*
      7b. Lateral sepals never spurred or saccate.
        8a. Dorsal sepal spurred ..... *Brownleea*
        8b. Dorsal sepal never spurred.
          9a. Lip-blade anchor-shaped, rarely rhomboid or reniform.
            10a. Lip with a prominent callus ..... *Ceratandra*
            10b. Lip without a callus ..... *Evotella*
          9b. Lip blade not anchor-shaped.
            11a. Dorsal sepal and petals forming a deeply globose hood ..... *Corycium*
            11b. Dorsal sepal and petals forming a shallow to flat galea ..... *Pterygodium*
    6b. Petals free from the dorsal sepal; lip never appressed to the stigma and generally patent at the base.
      12a. Lip complex, with an ascending basal part, flat middle part, and toothlike apex ..... *Schizodium*
      12b. Lip simple, rarely lobed or fimbriate.
        13a. Viscidium solitary or rarely paired; petals and lip fleshy; rostellum consisting only of a massive central lobe ..... *Monadenia*
        13b. Viscidia paired or rarely fused; petals and lip not fleshy; rostellum two- or three-lobed.
          14a. Lip ovate, sessile or spathulate, the margins often fimbriate or lobed; petals strongly falcate; leaves grasslike ..... *Herschelianthe*
          14b. Plants not as above ..... *Disa*

Literature Cited

Barthlott, W. 1976. Morphologie der Samen von Orchideen iin Hinblick auf taxonomische und funktionelle Aspekte. Proceedings of the Eighth World Orchid Conference 1976: 444–455.

Bentham, G. & J. D. Hooker. 1883. Genera Plantarum, vol. 3. L. Reeve, London.

Bolus, H. 1882. Notes on some Cape orchids. J. Linn. Soc., Bot. 19: 233–238.

———. 1888. The orchids of the Cape Peninsula. Trans. S. African Philos. Soc. 5: 1–201.

———. 1893 1896. Icones Orchidearum Austro-Africanarum Extratropicarum, Vol. 1. Wesley & Son, London.

———. 1911. Icones Orchidearum Austro-Africanarum Extratropicarum, Vol. 2. Wesley & Son, London.

———. 1913. Icones Orchidearum Austro-Africana-

rum Extratropicarum, Vol. 3. Wesley & Son, London.
———. 1918. The orchids of the Cape Peninsula, ed. 2. Darter Bros., Cape Town.
BURNS-BALOGH, P. 1983. A theory on the evolution of the exine in the Orchidaceae. Amer. J. Bot. 70: 1304–1312.
——— & V. A. FUNK. 1986. A phylogenetic analysis of the Orchidaceae. Smithsonian Contr. Bot. 61: 1–79.
CARPENTER, J. M. 1988. Choosing among multiple equally parsimonious cladograms. Cladistics 4: 291–296.
CHASE, M. W. & J. S. PIPPEN. 1988. Seed morphology in the Oncidiinae and related subtribes (Orchidaceae). Syst. Bot. 13: 313–323.
CHESSELET, P. C. 1989. Systematic Implications of Leaf Anatomy and Palynology in the Disinae and Coryciinae (Orchidaceae). M.Sc. Thesis, University of Cape Town.
——— & H. P. LINDER. 1993. Pollen morphology of the Diseae (Orchidoideae; Orchidaceae). Grana 32: 101–110.
CLIFFORD, H. T. & W. K. SMITH. 1969. Seed morphology and classification of Orchidaceae. Phytomorphology 19: 133–139.
DARWIN, C. 1888. The Various Contrivances by which Orchids are Fertilised by Insects, 2nd ed. John Murray, London.
DRESSLER, R. L. 1979. The subfamilies of the Orchidaceae. Selbyana 5: 197–206.
———. 1981. The Orchids—Natural History and Classification. Harvard Univ. Press, Cambridge, Massachusetts, and London.
———. 1986. Recent advances in orchid phylogeny. Lindleyana 1: 5–20.
———. 1990. The Neottieae in orchid classification. Lindleyana 5: 102–109.
FARRIS, J. S. 1969. A successive approximations approach to character weighting. Syst. Zool. 18: 374–385.
———. 1988. Hennig86 Reference. Published privately.
FELSENSTEIN, J. 1985. 1988. Confidence limits on phylogenies: An approach using the bootstrap. Evolution 39: 783–791.
FUNK, V. A. 1982. The systematics of *Montanoa* (Asteraceae, Heliantheae). Mem. New York Bot. Gard. 36: 1–133.
———. 1985a. Phylogenetic patterns and hybridization. Ann. Missouri Bot. Gard. 72: 681–715.
———. 1985b. Cladistics and generic concepts in the Compositae. Taxon 34: 72–80.
HALL, A. V. 1982. A revision of the southern African species of *Satyrium*. Contrib. Bolus Herb. 10: 1–137.
HEALEY, P. L., J. D. MICHAUD & J. ARDITTI. 1980. Morphometry of orchid seeds. III. Native California and related species of *Goodyera, Piperia, Platanthera* and *Spiranthes*. Amer. J. Bot. 67: 508–519.
HUMPHRIES, C. J. 1981. Cytogenetic and cladistic studies in *Anacyclus* L. (Compositae: Anthemideae). Nordic J. Bot. 1: 83–96.
HUNT, P. F. 1968. *Pterygodium*, Orchidaceae, part 1. Pp. 216–230 *in* E. Milne-Redhead & R. M. Polhill (editors), Flora of Tropical East Africa. Crown Agents for Oversea Governments and Administrations, London.
KAPLAN, D. R. 1975. Comparative developmental evaluation of the morphology of unifacial leaves in the monocotyledons. Bot. Jahrb. Syst. 95: 1–105.
KRAENZLIN, F. 1899–1900. Orchidacearum Genera et Species. Mayer & Müller, Berlin.
KURZWEIL, H. 1987a. Developmental studies in orchid flowers. I: Epidendroid and vandoid orchids. Nordic J. Bot. 7: 427–442.
———. 1987b. Developmental studies in orchid flowers. II: Orchidoid species. Nordic J. Bot. 7: 443–451.
———. 1988. Developmental studies in orchid flowers. III: Neottioid species. Nordic J. Bot. 8: 271–282.
———. 1989. Floral morphology and ontogeny in *Huttonaea pulchra*. Lindleyana 4: 1–5.
———. 1990. Floral morphology and ontogeny in Orchidaceae subtribe Disinae. J. Linn. Soc., Bot. 102: 61–83.
———. 1991. The unusual structure of the gynostemium in the Orchidaceae-Coryciinae. Bot. Jahrb. Syst. 112: 273–293.
———. 1993a. The remarkable anther structure of *Pachites bodkinii* (Orchidaceae). Bot. Jahrb. Syst. 114: 561–569.
———. 1993b. Seed morphology in southern African Orchidoideae (Orchidaceae). Pl. Syst. Evol. 185: 229–247.
——— & H. P. LINDER. 1991. A comparative study of the floral morphology in the genus *Disperis* (Orchidaceae). Beitr. Biol. Pflanzen 66: 433–477.
———, ——— & P. CHESSELET. 1991. The phylogeny and evolution of the *Pterygodium-Corycium* complex (Coryciinae, Orchidaceae). Pl. Syst. Evol. 175: 161–223.
LINDER, H. P. 1981a. Taxonomic studies on the Disinae: 1. A revision of the genus *Brownleea* Lindl. J. S. African Bot. 47: 13–48.
———. 1981b. Taxonomic studies on the Disinae: 2. A revision of the genus *Schizodium* Lindl. J. S. African Bot. 47: 339–371.
———. 1981c. Taxonomic studies on the Disinae. III. A revision of *Disa* Berg. excluding sect. *Micranthae* Lindl. Contrib. Bolus Herb. 9: 1–370.
———. 1981d. Taxonomic studies in the Disinae. V. A revision of the genus *Monadenia* Lindl. Bothalia 13: 339–363.
———. 1981e. Taxonomic studies in the Disinae. VI. A revision of the genus *Herschelia* Lindl. Bothalia 13: 365–388.
———. 1981f. Taxonomic studies in the Disinae. IV. A revision of *Disa* Berg. sect. *Micranthae* Lindl. Bull. Jard. Bot. Natl. Belg. 51: 255–346.
———. 1985 Notes on the orchids of southern tropical Africa. I: *Brownleea* and *Herschelia*. Kew Bull. 40: 125–129.
———. 1986 Notes on the phylogeny of the Orchidoideae, with particular reference to the Diseae. Lindleyana 1: 51–64.
———. 1989. *Satyridium rostratum*. Fl. Pl. Africa 50: pl. 1993.
———. 1991. Confidence limits in phylogenies: An example from the African Restionaceae. Taxon 40: 253–266.
——— & H. KURZWEIL. 1990. Floral morphology and phylogeny of the Disinae (Orchidaceae). J. Linn. Soc., Bot. 102: 287–302.

LINDLEY, J. 1830–1840. Genera and Species of Orchidaceous Plants. Ridgeways, London.

MANNING, J. C. & H. P. LINDER. 1992. Pollinators and evolution in *Disperis* (Orchidaceae), or why are there so many species? S. African J. Sci. 88: 38–49.

MARLOTH, R. 1895. The fertilisation of *Disa uniflora* Berg. by insects. Trans. S. African Philos. Soc. 8: xciii–xcv.

PFITZER, E. 1889. Orchidaceae. *In:* A. Engler & K. Prantl (editors), Die Natürlichen Pflanzenfamilien 2(6): 53–96. Engelmann, Leipzig.

PHIPPS, J. B., K. R. ROBERSON, J. R. ROHRER & P. G. SMITH. 1991. Origins and evolution of Subfam. Maloideae (Rosaceae). Syst. Bot. 16: 303–332.

RASMUSSEN, F. N. 1982. The gynostemium of the neottioid orchids. Opera Bot. 65: 1–96.

RAUSCHERT, S. 1983. Beitrag zur Nomenklatur der Orchidaceae. Feddes Repert. 94: 433–471.

ROLFE, R. A. 1898. Orchideae. *In:* W. T. Thiselton-Dyer (editor), Flora of Tropical Africa VII: 12–292.

———. 1912 1913. Orchidaceae. *In:* W. T. Thiselton-Dyer (editor), Flora Capensis, Vol. V, Sect. 3. L. Reeve, London.

RUDALL, P. 1990. Comparative leaf morphogenesis in Iridaceae. Bot. Jahrb. Syst. 112(2): 141–260.

SANDERSON, M. J. 1989. Confidence limits on phylogenies: The bootstrap revisited. Cladistics 5: 113–129.

SCHELPE, E. A. 1966. An Introduction to the South African Orchids. Purnell & Sons, Cape Town, Johannesburg.

SCHILL, R. & W. PFEIFFER. 1977. Untersuchungen an Orchideenpollinien unter besonderen Berücksichtigung ihrer Feinskulpturen. Pollen & Spores 19: 5–118.

SCHLECHTER, R. 1898. Monographie der Disperideae. Bull. Herb. Boissier ser. 1, 6: 800–821, 846–859, 905–955.

———. 1901. Monographie der Diseae. Bot. Jahrb. Syst. 31: 134–313.

———. 1926. Das System der Orchidaceen. Notizbl. Bot. Gart. Berlin-Dahlem 9: 563–591.

SENGHAS, K. 1973–1974. Orchidoideae. *In:* F. G. Brieger, R. Maatsch & K. Senghas. 1971ff., Die Orchideen. Rudolf Schlechter, 3rd ed. Berlin, Hamburg.

STEINER, K. M. 1989. The pollination of *Disperis* (Orchidaceae) by oil-collecting bees in southern Africa. Lindleyana 4: 164–183.

STEVENS, P. F. 1985. The genus concept in practice—But for what practice? Kew Bull. 40: 457–465.

———. 1991. Character states, morphological variation, and phylogenetic analysis: A review. Syst. Bot. 16: 553–583.

STEWART, J., H. P. LINDER, E. A. SCHELPE & A. V. HALL. 1982. Wild Orchids of Southern Africa. MacMillan South Africa, Johannesburg.

SUMMERHAYES, V. S. 1968. Orchidaceae (Part 1). *In:* E. Milne-Redhead & R. M. Polhill (editors), Flora of Tropical East Africa. Crown Agents for Oversea Governments and Administrations, London.

SWARTZ, O. 1800. Orchidemes slagter orch arter upstallde. Kongl. Vetense. Acad. Nya Handl. 31: 202–254.

SWOFFORD, D. L. 1993. PAUP: Phylogenetic Analysis Using Parsimony, Version 3.1. A User's Manual. Illinois Natural History Survey, Champaign.

SZLACHETKO, D. L. 1991. New taxa within the order Orchidales. Folia Geobot. Phytotax. 26: 315–329.

TOHDA, T. 1983. Seed morphology in Orchidaceae I. *Dactylorchis*, *Orchis*, *Ponerorchis*, *Chondradenia* and *Galeorchis*. Sci. Rep. Tohoku Imp. Univ., Ser. 4, Biol. 38: 253–268.

TRIMEN, R. 1864. On the fertilization of *Disa grandiflora*, J. Linn. Soc., Bot. 7: 144–147.

VERDCOURT, B. 1968. *Disperis*, Orchidaceae (part 1). Pp. 216–230 *in* E. Milne-Redhead & R. M. Polhill (editors), Flora of Tropical East Africa. Crown Agents for Oversea Governments and Administrations, London.

VOGEL, S. 1959. Organographie der Blüten Kapländischer Ophrydeen, mit Bemerkungen zum Koaptations-Problem. Akad. Wiss. Abh. Math.-Naturwiss. Kl. 2: 268–532.

WAGNER, W. L., R. E. STOCKHOUSE & W. M. KLEIN. 1985. The systematics and evolution of the *Oenothera caespitosa* species complex (Onagraceae). Monogr. Syst. Bot. Missouri Bot. Gard. 12: 1–103.

WEALE, M. J. P. 1873. Some observations on the fertilisation of *Disa macrantha*. J. Linn. Soc., Bot. 13: 45–47.

WEBER, A. 1980. Die Homologie des Perigons der Zingerberaceen. Ein Beitrag zur Morphologie und Phylogenie des Monokotylen-Perigons. Pl. Syst. Evol. 133: 149–179.

WERDELIN, L. 1989. We are not out of the woods yet—A report from a Nobel symposium. Cladistics 5: 192–200.

WILDHABER, O. J. 1972. Zur Karpologie von *Orchis*. *In:* K. Senghas & H. Sundermann (editors), Probleme der Orchideengattung *Orchis*. Jahresber. Naturwiss. Vereins Wuppertal 25: 61–66.

WILEY, E. O. 1981. Phylogenetics. The Theory and Practice of Phylogenetic Systematics. John Wiley & Sons, New York.

WILLIAMSON, G. 1977. The Orchids of South Central Africa. J. M. Dent & Sons, London.

ZIEGLER, B. 1981. Mikromorphologie der Orchideensamen unter Berücksichtigung Taxonomischer Aspekte. Ph.D. Thesis, Ruprecht Karls Universität, Heidelberg.

TAXONOMY OF *THERMOPSIS* (FABACEAE) IN NORTH AMERICA[1]

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ABSTRACT

Comprehensive reevaluation of both herbarium specimens and field observations of the North American *Thermopsis* leads to our recognition of 10 species. Three species occur in the southern Appalachians: *T. villosa*, *T. mollis*, and *T. fraxinifolia*. The Rocky Mountains and intermountain regions are populated by the relatively variable and widespread species *T. divaricarpa*, *T. montana*, and *T. rhombifolia*. The Pacific coastal mountains of California are dominated by the variable *T. californica* (with three infraspecific taxa), which gives way to *T. gracilis* in northern California and western Oregon. *Thermopsis macrophylla* and *T. robusta* have restricted ranges in California.

Widely distributed throughout the western and southeastern United States, *Thermopsis* is a conspicuous, often weedy genus. Though it is a herbaceous plant, its relatively large habit and stunning racemes of golden or bright yellow flowers and flattened, rattling pods have no doubt contributed to its early and thorough collection. These factors, perhaps, should have led to a clear understanding of its systematics, but a lack of diagnostic characters within the genus, morphological intergradation, and possible hybridization have complicated the taxonomy of *Thermopsis*. Modern treatments (e.g., Isely, 1981) include from 4 to 10 species in North America, though over 20 specific names have been proposed.

The current study is based on over 20,000 km of roadside field study in North America (spanning 25 years for B. Turner), greenhouse studies (by M. Mendenhall), and the examination of approximately 6000 herbarium specimens (by all of the authors). We find 10 species of *Thermopsis* in North America. This treatment differs from earlier evaluations primarily in the rank and affiliations of taxa in the western United States. While an extreme perspective would combine the western taxa into two highly variable species, we recognize four species in the Pacific coastal states, three of which have restricted ranges, and three widely distributed species in the Rocky Mountain and intermountain regions. The three long-recognized species of the southeastern United States are maintained.

The following herbaria have generously supplied the approximately 6000 specimens used in this study (number of sheets loaned given in parentheses): ARIZ (113), CAS (516), COLO (181), F (193), GH (511), JEPS (16), LL (15), MO (444), MONTU (91), NCU (112), ND (99), NEBC (3), NY (715), ORE (78), OSC (85), PE (52), PH (193), POM (75), RM (611), RSA (302), TENN (71), TEX (163), UC (401), US (419), UT (83), WS (161), WTU (200).

HISTORY OF THE GENUS

Thermopsis (Greek "thermos" = lupine + "opsis" = appearance) was originally included in *Sophora* by Linnaeus (1753). Willdenow (1799) placed the taxon in *Podalyria*. In 1811, Robert Brown erected *Thermopsis* based upon *Sophora lupinoides* L. Brown renamed the latter *Thermopsis lanceolata*, which is contrary to the present Code of Botanical Nomenclature (Greuter et al., 1988); the name *Thermopsis lupinoides* (L.) Link, erected in 1821 and recognized still, precludes the use of this specific epithet for the type species of the genus. In 1818, Nuttall called the genus *Ther-*

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mia. Rafinesque erected the genera *Scolobus* and *Drepilia* in 1819, both based on specimens of *Thermopsis rhombifolia*.

Larisey (1940) revised the North American *Thermopsis* because she saw considerable "taxonomic confusion," which she eventually ascribed to "bibliographical" problems. She distilled 22 published names to 10 species by reducing the 4 southeastern species to 3 and 18 western species to 7. St. John (1941) responded to Larisey's revision with some notes on nomenclature and morphology. Though variously treated in regional floras, the most significant work on *Thermopsis* since its revision has been Isely's (1981) treatment in *Leguminosae of the United States*. Isely drastically reduced the number of species in *Thermopsis*, primarily by lowering these to varietal status. He perceived variation in the western taxa as too trivial to support the specific rank. Furthermore, he saw that "all taxa are seemingly confluent with those geographically contiguous." His views were not universally accepted at the time (Turner, 1982), and our findings support recognition of most of these taxa as separate species.

Thermopsis is the largest and most widespread member of the small tribe Thermopsideae, which consists of about 46 species in 6 genera (Turner, 1981). All of these are restricted to temperate regions of the Northern Hemisphere. The tribe is characterized by ten free stamens and petiolate, trifoliate leaves. Though most of the genera are woody, the two herbaceous genera, *Baptisia* and *Thermopsis*, account for most of the species in the Thermopsideae. These two genera are united by many other morphological as well as secondary chemical characteristics. In fact, Larisey (1940) referred to *Thermopsis* as a western geographical supplement of *Baptisia*, though it seems more likely that one or several lines of *Baptisia* was derived from a *Thermopsis*-like ancestor (Turner, 1967). In fact, Cranmer & Turner (1967) offered *Baptisia* and *Thermopsis* as possible ancestors to the Genisteae on the basis of morphology, alkaloid chemistry, and geography. Since then, the woody Thermopsideae have been favored as close relatives to the Genisteae (Polhill, 1976; Turner, 1981).

Biogeography

Thermopsis occurs not only in North America; 13 species are found in Asia. The Asian species occur at elevations of 1500–4000 m from India northward to eastern Kazakhstan and southern Russia, eastward across China, Mongolia, and Russia, and beyond to Japan, far eastern Russia, and the North American coast of the Bering Sea. Most of the Asian species were treated by Shishkin (1945). Judging from the relative uniformity of the North American species, taxa ancestral to extant *Thermopsis* probably crossed Beringia into North America.

On the North American continent, *Thermopsis* is distributed throughout the western states and in the southern Appalachian foothills. *Thermopsis villosa* and *T. fraxinifolia* are native to Tennessee, Georgia, and the Carolinas where they occur in woodlands at elevations of 700–1600 m. Also in the east is *T. mollis*, which is found in the same states as *T. villosa* and *T. fraxinifolia* as well as in Virginia, but at lower elevations, typically between 300 and 800 m.

In western North America, *Thermopsis* occurs both in the Rocky Mountain and intermountain regions as well as in the Pacific coastal states. *Thermopsis montana* is the most widely distributed species; it is found as two intergrading, regional varieties in the intermountain region from 300 to 3200 m. Morphology and habitat are variable throughout its range from Montana southward to Arizona and New Mexico and northwestward to Wyoming, Idaho, Oregon, and Washington. Found at relatively low elevations, 1000–2000 m, is *T. rhombifolia*. Although this taxon can be found from Alberta and Saskatchewan to New Mexico, it is largely restricted to alluvial soils in dry grasslands. *Thermopsis divaricarpa* occurs at middle to high elevations, 2000–3000 m, in the Rocky Mountains from Wyoming to New Mexico, in mesophytic conifer forests.

Most of the *Thermopsis* in the Pacific coastal states is found in California. In central California, *T. californica* var. *californica* is common in chaparral west of the Sierra Nevadas up to 1000 m elevation. In northwestern California and southern Oregon, *T. gracilis* is dominant and occurs at low elevations, to 1200 m, in mesophytic forests. The remaining taxa in the extreme west have restricted distributions within California. *Thermopsis californica* var. *argentata* has a disjunct range in northeasternmost and southwestern California; this taxon grows at high elevations, 1200–2200 m, in montane chaparral and pine forests. *Thermopsis macrophylla* is known only from the western side of Santa Ynez Peak in Santa Barbara County. Our study of type material indicates that this name has been erroneously applied to the more common *T. californica* var. *californica*. Unlike the latter, *T. macrophylla* is highly localized, relatively uniform, and strikingly robust. Equally impressive in habit is *Thermopsis robusta*, which is found only in

TABLE 1. Chromosome numbers in *Thermopsis*. Counts listed with voucher only are original meiotic counts by the junior author (T); vouchers on deposit at TEX.

	2*n* number	Reference/voucher
Asian species		
T. alterniflora Regel	18	Federov (1969)
T. barbata Benth. ex Royle	18	Chen et al. (1992)
T. chinensis Benth. ex S. Moore	18	Yeh et al. (1986)
T. chinensis Benth. ex S. Moore	18	Chen et al. (1992)
T. lanceolata R. Br.	18	Mesicek & Sojak (1969)
T. lanceolata R. Br.	18	Chen et al. (1992)
T. licentiana E. Peter	18	Chen et al. (1992)
T. lupinoides (L.) Link [as *T. fabacea* (Pallas) DC.]	18	Federov (1969)
T. lupinoides (L.) Link	18	Probatova & Sokolovskaya (1981)
T. mongolica Czefr.	18	Mesicek & Sojak (1969)
T. przewalskii Czefr.	18	Chen et al. (1992)
American species		
T. californica var. *argentata*	18	**California**: Modoc Co., *T. 5813, T. 5816*
T. divaricarpa	36	**Colorado**: Jefferson Co., *T. 5636*
T. divaricarpa	36	**Colorado**: Las Animas Co., *T. 5772*
T. divaricarpa	36	**Colorado**: Saguache Co., *Tomb 649*
T. gracilis	36	**Oregon**: Lane Co., *T. 5797*
T. macrophylla	18	**California**: Santa Barbara Co., *T. 5820*
T. montana (var. *montana*?)	18	Federov (1969)
T. montana (var. *montana*?)	18	**Colorado**: Summit Co., Gillett (1975)
T. montana var. *montana*	18	**Colorado**: Saguache Co., *T. 5775*
T. montana var. *montana*	18	**Idaho**: Owyhee Co., *T. 5798*
T. montana var. *montana*	18	**Nevada**: Elko Co., *T. 5795, T. 5796*
T. montana var. *montana*	18	**Utah**: Wasatch Co., *T. 5794*
T. rhombifolia	18	CANADA: **Saskatchewan,** Ledingham (1957)
T. rhombifolia	18	CANADA: **Saskatchewan,** Taylor (1967)
T. rhombifolia	18	CANADA: **Saskatchewan,** Federov (1969)
T. rhombifolia	18	CANADA: **Manitoba**, Löve & Löve (1982)
T. rhombifolia	18	**Colorado**: Huerfano Co., *T. 5773*
T. villosa	18	Zhukova (1967)

Humboldt and Siskyou Counties of northwestern California along ridgetops to 1500 m. Finally, *Thermopsis californica* var. *semota* is restricted to the woodlands of San Diego County.

CHROMOSOME NUMBERS

The first chromosome counts for *Thermopsis* were obtained by Russian workers in 1931 (Federov, 1969). These were obtained for the Asian species, *T. alterniflora*, and the American species, *T. montana*; both were found to have somatic counts of $2n = 18$. Subsequent counts for all of the species investigated have also been on a base of $x = 9$ (Table 1).

Polyploids ($2n = 36$) are known in only two species, *T. gracilis* and *T. divaricarpa*, both American, the former occurring in northern California and adjacent Oregon, the latter occurring in the front range of the Rocky Mountains, mostly in central Colorado. Polyploidy is believed to have arisen independently in the two taxa, largely because of their geographical isolation from one another. Relatively few counts have been recorded for these two taxa, however, and it remains to be seen if such counts will hold throughout their respective distributions.

A base chromosome number of $x = 9$ is also found in the closely related *Baptisia*, a genus of about 17 species that is confined to lower elevations of the southeastern United States (see Isely, 1981, for overview). To date, no polyploids have been reported for *Baptisia*.

SECONDARY CHEMISTRY (MICROMOLECULES)

Unlike in *Baptisia*, flavonoids and alkaloids have been of limited usefulness in characterizing interspecific variation in *Thermopsis*. On the basis of quinolizidine alkaloid distribution, Salatino & Gott-

lieb (1980) were able to divide *Thermopsis* into two phyletic groups, the Asian and the North American species. A comprehensive phylogeny, however, has not yet been proposed since alkaloid and flavonoid data are insufficient (Turner, 1967; Dement & Mabry, 1975) and contradictory (Balandrin et al., 1982).

Secondary chemical data have been used, nonetheless, to place the genus within a phylogenetic reconstruction of a larger scale. Based on quinolizidine alkaloid distributions (Salatino & Gottlieb, 1980), most of the Thermopsideae probably arose from "*Sophora*-like taxa" (Turner, 1981). Furthermore, based on serological cross reactivity of seed proteins (Cristofolini, 1987), general morphology (Polhill, 1976), and phytochemistry (Faugeras & Paris, 1968; Harborne, 1969; Salatino & Gottlieb, 1983), the woody Thermopsideae gave rise in turn to the Genisteae (Bisby, 1981; Cristofolini & Feoli-Chiapella, 1984; Polhill, 1976; Turner, 1981).

Morphology

Thermopsis has been commonly referred to as "false lupine," "buckbean," "goldenpea," "golden banner," and "bush pea." Though the flower has inspired several of these names, it varies little within the genus and is not especially useful for specific delimitation. There are slight variations in flower size and petal shape, which often appear constant within a taxon, but these are so minor as to be of limited usefulness for identification purposes.

Fruit characters are used to distinguish between *Thermopsis* and *Baptisia*; compressed pods are mostly found in the former and inflated in the latter. The posture and shape of the mature pods vary diagnostically within *Thermopsis* as well. The fruit may be erect, ascending, or divergent from the raceme axis. There seems to be no geographical correlation to pod posture; *T. californica* and *T. macrophylla* of California, *T. montana* of the intermountain region, and *T. villosa* of the Appalachians all have erect or ascending fruits, and irregularly to strongly divergent pods are found in the remaining species. Likewise, pod shape varies among species of the same region, though pods that are strongly divergent will also be arcuate or annular. Isely (1981) noted that ovule number is characteristic within regions of the generic distribution. Indeed, we found that in southern California *Thermopsis* typically has 5–9 ovules and in northern California 8–14 ovules. The Rocky Mountain and intermountain species have 10–18 ovules and the Appalachian species have 12–16. These figures do overlap, however, and can be called trends at best.

Vegetative characters are often quantitative with much variation around average proportions. Nevertheless, certain characters have wide diagnostic application within the genus. Plant height, leaf size and shape, and pubescence have some utility, though there is overlap between taxa, especially varieties. Although the leaf apices may differ on a single plant, the number of leaf veins and their visibility are sometimes useful. The stipules are of two types: the lower stipules in all taxa are scarious and do not subtend leaves, the upper are foliaceous and blade-bearing. The foliaceous stipules differ diagnostically in shape, ranging from lanceolate to broadly ovate, and in size, growing to 9 cm long and 6 cm wide. Inflorescence bracts, likewise, vary in shape and size and also in persistence. Racemes may bear short or long pedicels, and these may be pubescent or not. In addition, the flowers may be scattered along the axis or may be inserted in whorls, even where the flowers are not especially dense. Within the flowers, calyx proportions may confirm identity but are not especially useful alone.

Most *Thermopsis* species propagate by rhizomes, sometimes, as in *T. mollis* and *T. rhombifolia*, forming extensive clonal populations. Otherwise, the plants are supported by thick, perennial rootstocks. It is often impossible to confirm the presence of rhizomes on herbarium specimens, especially of large plants, which typically show just enough of the apical structures to fit on a herbarium sheet. Yet field observations indicate that a given taxon will have a tendency to form rhizomes or not, and this character should be preserved during collection and noted for identification.

For stems, branches, and fruits, the angle of insertion is described as erect, ascending, divergent, or spreading. Distinctions between these terms may be confusing. In the following descriptions, "erect" indicates vertical posture or nearly so and little or no curvature at the point of attachment while "ascending" indicates an angle of attachment up to 50° from vertical often with upward curvature at the point of attachment. Though "spreading" and "divergent" are roughly synonymous, here "spreading" is used for branches and "divergent" is used for fruits.

Species and Varietal Concepts

As is discussed above, the primary difference in the various treatments of *Thermopsis* has been in the rank of the taxa. In this treatment, the specific rank has been chosen to express what we perceive

to be evolutionarily independent taxa. We have inferred this from morphological evidence of reproductive independence both from herbarium specimens and observations of populations in the field. For example, although occasional sympatric hybridization is suspected between members of *T. divaricarpa* and both *T. montana* and *T. rhombifolia*, there is no evidence that these hybrids have stabilized and persisted. Nevertheless, Isely occasionally, if not often, saw intergradation, where we, like Larisey, see none. We attribute the resolution of our perception to the extensive field and herbarium work that is the basis of this study.

Taxonomic Treatment

Thermopsis R. Br., Hortus Kew., ed. 2, III. 3. 1811. TYPE: *Sophora lupinoides* L. = *Thermopsis lanceolata* R. Br. = *Thermopsis lupinoides* (L.) Link.

Thermia Nutt., Gen. N. Amer. Pl. 1: 282. 1818. TYPE: *Thermia rhombifolia* (Pursh) Nutt.

Scolobus Raf., Amer. Monthly Mag. Crit. Rev. 4: 193. 1819. TYPE: *Scolobus rhombifolius* (Nutt. ex Pursh) Raf.

Drepilia Raf., N. Fl. 2: 52. 1836 [1837]. TYPE: *Drepilia rhombifolia* (Nutt. ex Pursh) Raf.

Perennial herbs, usually rhizomatous; stems erect or ascending, few-branched to well-branched, branches ascending or spreading; plants glabrate to variously pubescent, unarmed. Leaves petiolate, trifoliolate, not glandular-punctate; stipules usually persistent, foliaceous or nearly so, dimorphic, the lowermost amplexicaul, scarious, and not blade-bearing, the rest broadly ovate to lanceolate and subtending leaves, to 6(–9) cm long, to 3(–6) cm wide, smaller and narrower on branches; leaflets subpetiolulate, narrowly elliptic to obovate, 2–8(–10) cm long, margins entire; estipellate. Inflorescences terminal (lateral) racemes, commonly solitary, flowers few to numerous, scattered or whorled; bracts deciduous or persistent, widely ovate to lanceolate, acute to acuminate; bracteoles absent; pedicels 2–17 mm long. Flowers papilionaceous; calyx campanulate, appearing 4-lobed, subequal, the upper lobe double, broader, and slightly longer than the others, truncate to emarginate, the lower lobes deltoid to lanceolate; corolla yellow; banner very widely ovate, shorter than wings and keel, cleft (emarginate and short mucronate), claw cuneate to oblong, replicate-reflexed; wings usually asymmetric, elliptic to oblong-rhombic, auriculate, ± length of keel, not adnate to keel, claw narrowly oblong; keel asymmetrically oblong-elliptic to carinate, auriculate, posteriorly fused, without a beak, claw narrowly oblong; stamens 10, free, uniform; anthers dorsifixed; pistil short-stipitate; ovary oblong, usually longer than style, villosulous; ovules 5–15; style glabrous; stigma minute. Legumes persistent, erect, ascending, or divergent, tan to brown, narrowly elliptic, laterally compressed, straight, arcuate, or rarely annular, margins straight or, as a consequence of ovule abortion, sinuate or lomentaceous; pericarp chartaceous, not elastic, variously pubescent; stipe 2–4 mm long; fruits slowly dehiscent, valves separating from apex through both sutures. Seeds (1–)3–10 per fruit, tan to brown-black, oblong to reniform, often with a minute, membranaceous rim-aril. Base chromosome number, $x = 9$.

Diagnosis and relationships. *Thermopsis* is a member of the Thermopsideae Yakovlev (Bot. Žurn. 57: 585–595, 1972), by virtue of its free stamens and palmately trifoliate, petiolate leaves. Although *Thermopsis* is loosely allied with all other Thermopsideae, it is very similar morphologically to *Baptisia*, the other prominent North American member of the tribe. Fruiting *Thermopsis* can be distinguished readily from *Baptisia*. The pods of North American *Thermopsis* are flattened, while those of *Baptisia* are inflated.

As detailed above, *Thermopsis* is found in Asia and North America. In North America four species occur in the Pacific coastal states, three occur in the Rocky Mountains and intermountain regions, and three are found in the southern Appalachians.

Key to Species

1a. Plants of southern Appalachian foothills.
  2a. Stipules on primary axis more than 1 cm wide; pedicels less than 3 mm long; pods erect, densely villous ..... 10. *Thermopsis villosa*
  2b. Stipules on primary axis less than 1 cm wide; pedicels more than 3 mm long; pods irregularly divergent, pubescent or glabrate.
    3a. Plants rhizomatous; pedicels villosulous and shorter than bracts; racemes terminal; mostly piedmont, 300–800 m ..... 6. *Thermopsis mollis*
    3b. Plants from a single woody rootstock; pedicels glabrate and at least as long as bracts; racemes terminal or lateral; montane, usually 1000–2000 m ..... 3. *Thermopsis fraxinifolia*
1b. Plants of Rocky Mountains, intermountain regions, and Pacific coastal states.
  4a. Plants tomentose or sericeous throughout; flowers usually in whorls of 3–5; California.

5a. Plants mostly 3–8 dm tall; leaflets mostly 3–7 cm long; pods ascending, usually with several or more abortive ovules ..... 1. *Thermopsis californica*
5b. Plants mostly 10–20 dm tall; leaflets up to 11 cm long; pods ascending or divergent, usually with well-developed ovules.
6a. Pods ascending and straight; pedicels 2.5–4 mm long; lateral leaf veins 6–8 pairs; Santa Ynez Mts. of California ..... 5. *Thermopsis macrophylla*
6b. Pods divergent and arcuate; pedicels 4–8 mm long; lateral leaf veins 9–12 pairs; Humboldt and Siskiyou Counties of northwestern California ..... 9. *Thermopsis robusta*

4b. Plants glabrate to pubescent; flowers usually scattered; Pacific coastal mountains north of 40°N latitude, and more central portions of the western United States and adjacent Canada.
7a. Pods erect and straight ..... 7. *Thermopsis montana*
7b. Pods divergent and straight, arcuate, or annular.
8a. Branches spreading, strongly zigzagged; leaflets more than 2 cm wide, sometimes emarginate; petioles more than 2.5 cm long; pods straight; western Oregon and northern California ..... 4. *Thermopsis gracilis*
8b. Branches ascending, weakly to moderately zigzagged; leaflets less than 2 cm wide, not emarginate; petioles less than 2.5 cm long; pods usually arcuate or annular; northern and eastern Rocky Mountains and adjacent Great Plains.
9a. Plants 3 9 dm tall; leaflets more than 3 cm long, lateral veins 7–10 pairs; stipules ovate to narrowly elliptic; flowers 2.5–3.0 cm long; pods straight to arcuate ..... 2. *Thermopsis divaricarpa*
9b. Plants mostly 1–3 dm tall; leaflets less than 3 cm long, lateral veins 5–7 pairs; stipules usually widely ovate; flowers 1.6–2.1 cm long; pods strongly arcuate to annular ..... 8. *Thermopsis rhombifolia*

1. Thermopsis californica S. Watson, Proc. Amer. Acad. Arts 11: 126. 1876. TYPE: U.S.A. California: Marin Co., Corte Madera, *J. M. Bigelow* 1854 (lectotype, selected here, NY; probable isolectotypes, NY, PH, US).

Plants robust, (2.5)3–8 dm tall, sericeous or tomentose; stems slender, erect, clustered, well-branched, arising from rhizomes; branches ascending at 20–45°, weakly to strongly zigzagged. Leaflets elliptic or obovate, 3–7(–9) cm long, 1.2–4(–4.5) cm wide, obtuse or acute, silvery sericeous or tomentose to villous, lateral veins 6–9 pairs, conspicuously net-veined beneath; petioles 1–3.5 cm long; stipules persistent, widely ovate to lanceolate, 1.5–6.5 cm long, 0.7–5 cm wide, cuneate to amplexicaul, acuminate. Racemes 7–30(–35) cm long, with 10–40 flowers usually in whorls of 3–5; peduncles (2–)4–10 cm long; pedicels 2–6 mm long, sericeous or tomentose; bracts semipersistent, ovate to lanceolate, 6–15 mm long, 2.5–15(–20) mm wide. Flowers 1.5–2.0 cm long; calyx 5–10 mm long, 5–9 mm wide at the limb, lobes 2.5–5 mm long, as long or longer than tube; wing and keel petals oblong-elliptic to nearly reniform; ovary velutinous; ovules 5–11. Pods straight, ascending (irregularly divergent when young), 2–6(–7) cm long, (0.5–)0.6–0.9 cm wide, sericeous, tomentose, or velutinous. Seeds 1–6(–10), oblong with a short rostrum, 4–5.5 mm long, 2.5–4 mm wide.

Three varieties are recognized within *Thermopsis californica* as follows:

KEY TO VARIETIES OF *THERMOPSIS CALIFORNICA*

1a. Stipules widely ovate to ovate, to 5.0 cm wide; bracts to 15 mm wide; peduncles usually more than 6 cm long; pod pubescence of matted trichomes ..... 1b. *Thermopsis californica* var. *californica*
1b. Stipules ovate to lanceolate, to 2.5 cm wide; bracts to 6 mm wide; peduncles usually less than 6 mm long; pod pubescence of straight, appressed trichomes.
2a. Silvery sericeous throughout; wing and keel petals reniform; northeastern and southwestern California ..... 1a. *Thermopsis californica* var. *argentata*
2b. Villous to densely tomentose; wing and keel petals oblong-elliptic; restricted to San Diego Co., California ..... 1c. *Thermopsis californica* var. *semota*

1a. Thermopsis californica var. **argentata** (E. Greene) C. J. Chen & B. Turner, comb. nov. Basionym: *Thermopsis argentata* E. Greene, Erythea 3: 18. 1895. *Thermopsis gracilis* var. *argentata* (E. Greene) Jepson, Man. Fl. Pl. Calif. 515. 1925. *Thermopsis macrophylla* var. *argentata* (E. Greene) Jepson, Man. Fl. Pl. Calif. 2: 245. 1936. TYPE: U.S.A. California: Modoc Co., "Forestdale," *Baker* 1893 (lectotype, selected here, ND; isolectotypes, CAS, ND, NY, US).

In his protologue Greene cited a single collection from Modoc County, without locality, made by Milo S. Baker in 1893. Examination of material at ND reveals two sheets collected by Baker in the "Big Valley Mts." during June–August 1893. Both

sheets, which bear printed labels, were subsequently modified by hand-inkings so as to read August 1894. One sheet is clearly a mixture of plants collected in June (flowering sprig) and fall (late fruiting sprig). The other sheet is in late fruit. We have designated the latter as lectotype.

Plants (2.5–)3–5 dm tall, silvery sericeous throughout; branches weakly to moderately zigzagged. Leaflets obovate to elliptic, 3–6.5 cm long, 1.2–3.5 cm wide, obtuse to acute sometimes with a short mucro; petioles 1.3–2.1 cm long; stipules lanceolate to ovate, 1.5–6.0 cm long, 0.8–2.5 cm wide, cuneate to cordate. Racemes 8–20(–25) cm long, with 10–30 flowers; peduncles 4–7(–10) cm long; bracts ovate to lanceolate, 7–15 mm long, 2.5–5 mm wide. Calyx 7–9(–10) mm long, 5–8 mm wide at the limb, lobes 3.5–4.5(–5) mm long; banner cleft; wing and keel petals asymmetrically oblong-elliptic to reniform; ovules 8–11. Pods 3–6(–7) cm long, (0.5–)0.7–0.9 cm wide. Seeds 1–6, oblong, 4–5(–5.5) mm long, (2.5–)3.5–4 mm wide. Chromosome number, $2n = 18$.

Distribution and ecology (Fig. 1). Northeasternmost California (southeastern Siskiyou Co. and closely adjacent Shasta, Modoc, and Lassen cos.) and again in southwestern California (Kern, Ventura, Santa Barbara, and Los Angeles cos.), mostly interior montane chaparral and pine forests from 1200 to 2200 m; flowering May–June.

Representative specimens examined. U.S.A. **California:** Kern Co., Mt. Pinos, June 1905, *Hall 6378* (UC); Owens Valley and at Fort Tejon, *Horn* 1863 (NY). Lassen Co., ridge W of Nubieber, along California Hwy. 299, 26 June 1941, *Heller 16229* (MO, NY, WTU). Los Angeles Co., Santa Barbara, Liebre Ridge, N slope Liebre Mt., 15 Oct. 1923, *Hunt 5* (CAS, RM). Modoc Co., Forestdale, *Baker* 1894 (NY, PH, POM, RM, US); Forestdale, *Baker* 1899 (PH, UC); Forestdale, *Baker & Nutting* 1894 (CAS, GH, NY, RM, UC); 3 mi. NW of Lookout, 3 June 1968, *Turner 5813* (TEX); 14 mi. NW of Lookout, 3 June 1968, *Turner 5816* (TEX). Santa Barbara Co., San Rafael Mt., *Ford* 1887 (GH); Santa Ynez, Big Pine Mt., 7 Aug. 1936, *Peterson 303* (UC). Shasta Co., ca. 20 mi. W of Fall River Mills, 24 May 1940, *Hitchcock 6533* (NY, POM, UC, WTU); 1 mi. W of Dana, 2 June 1968, *Turner 5809* (TEX). Siskiyou Co., just E of Barnum Flat Reservoir, 3 June 1968, *Turner 5817* (TEX). Ventura Co., Fort Tejon, 19 June 1935, *Axelrod 434* (POM, UC); Mt. Pinos region, 28 June 1896, *Dudley & Lamb 4745* (CAS, UC); Lakes Ridge, above Maricopa Road on Matilija-Sespe divide, *Pollard* 1955 (CAS, COLO, TEX); 0.25 mi. NW of Reyes Peak, 23 Apr. 1934, *Sowder 393* (UC).

Thermopsis californica var. *argentata* differs from the more widespread, more variable variety *californica* in its smaller habit and closely appressed, silvery vestiture.

We are unable to distinguish between the northern and southern populations (Fig. 1). Isely (1981) applied the varietal name *argentata* (as part of his *T. macrophylla*) only to the more northern populations and included the southern populations in his *T. macrophylla* var. *macrophylla*. We agree with the assessment of Abrams (1944) that these disjunct interior populations represent a single taxon. At least we can find no characters by which to distinguish them though both are readily distinguished from varieties *californica* and *semota* by habit, vestiture, and petal shape.

1b. **Thermopsis californica** var. **californica**.

Thermopsis californica var. *velutina* E. Greene, Erythea 1: 81. 1893. *Thermopsis velutina* (E. Greene) E. Greene, Erythea 3: 19. 1895. *Thermopsis gracilis* var. *velutina* (E. Greene) Jepson, Man. Fl. Pl. Calif. 515. 1925. *Thermopsis macrophylla* var. *velutina* (E. Greene) Larisey, Ann. Missouri Bot. Gard. 27: 256. 1940. TYPE: U.S.A. California: Santa Clara Co., Mount Hamilton, *Greene* 1891 (lectotype, selected here, ND; isolectotype, ND).

In his protologue Watson did not cite specimens, but rather referred to the species as occurring in "Marin and Napa Counties, California, and probably southward." He did say that his *Thermopsis californica* was the same as what Torrey had referred to as "*T. macrophylla*" (Torrey, 1857) and *T.* "*fabacea*" (Torrey, 1859). Watson, in his protologue, indirectly suggested a lectotype with his citation of the Pacific Railroad Report in which Torrey cited a Bigelow collection from "Corte Madera," which is located in Marin County, California. We have selected the Bigelow collection from among contending lectotypes since the Torrey Herbarium collection at NY has the name *Thermopsis californica* Watson written on it, presumably in Watson's hand. Duplicates of the Bigelow collections were not found at GH, where Watson worked, nor were other contending lectotype collections annotated by him as belonging to *Thermopsis californica*.

Plants 3–8(–9) dm tall, sparsely to densely tomentose or villous; branches weakly to moderately zigzagged. Leaflets elliptic to obovate or rhombic, 3.5–7(–9) cm long, 2–4(–4.5) cm wide, obtuse to acute; petioles 1.5–3.5 cm long; stipules widely ovate to narrowly ovate, 2.5–6.5 cm long, 1.5–5.0 cm wide, cuneate to amplexicaul. Racemes

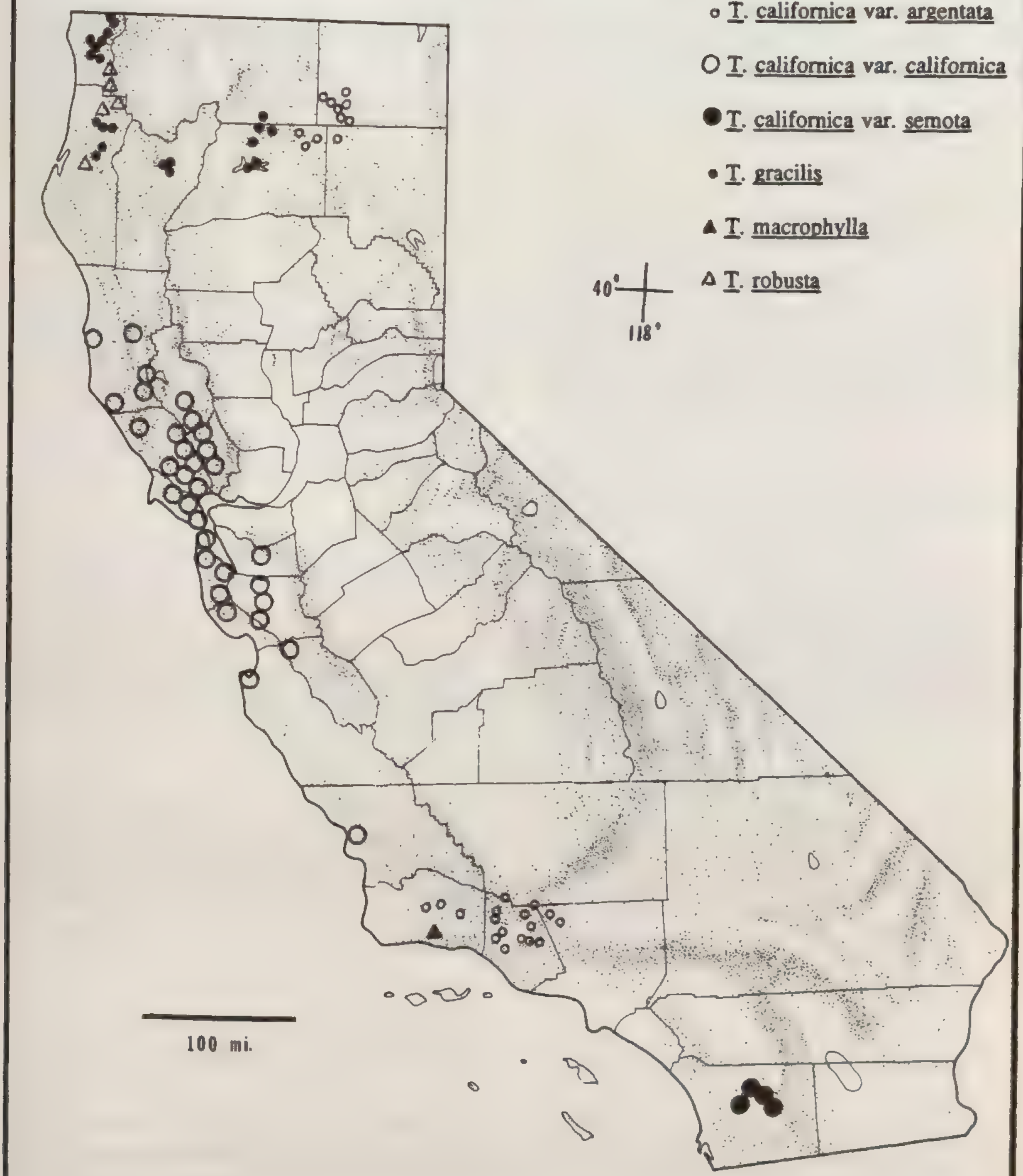

FIGURE 1. Distribution of *Thermopsis* in California: *T. californica* var. *argentata* (small open circles); *T. californica* var. *californica* (large open circles); *T. californica* var. *semota* (large closed circles); *T. gracilis* (small closed circles); *T. macrophylla* (closed triangle); *T. robusta* (open triangle).

10–30(–35) cm long, with 12–40 flowers; peduncles (4–)6–10 cm long; bracts widely ovate to nearly lanceolate, 6–15(–30) mm long, 3–15(–20) mm wide. Calyx 5–8(–9) mm long, 6–9 mm wide at the limb, lobes 2.5–5 mm long; banner cleft; wing and keel petals asymmetrically oblong-elliptic; ovules 5–8. Pods 3–5.5 cm long, 0.6–0.7 cm wide. Seeds 3–5(–10), oblong, 4 mm long, 2.8 mm wide.

Distribution and ecology (Fig. 1). Coastal regions of central California from 35 to 40°N latitude, mostly chaparral from near sea level to about 1000 m; flowering May–June.

Representative specimens examined. U.S.A. **California:** Alameda Co., hills E of Oakland, 1 Apr. 1929, *Tebbe 62* (UC). Lake Co., 9 mi. from Lower Lake on Monticello Road, 23 May 1937, *Ewan 10352* (COLO, MO, NY); flats near Morgan Valley, 25 May 1920, *Jepson 9034* (JEPS). Marin Co., Sausalito to Larkspur, 27 Apr. 1918, *Abrams 6882* (CAS, NY, US); San Rafael, dry hillsides, *Bolander* 1860–1867 (F, MO); Angel Island, San Francisco Bay, *Chestnut* 1888 (F, UC, US); Lagunitas, *Grinnell* 1918 (CAS, MO, NY, RM, UC); Tiburon, 17 Apr. 1938, *Rose 38146* (GH, MO, NY, WTU, UC). Mendocino Co., 5 mi. E of Point Arena, 29 May 1939, *Rose 39184* (GH, MO, NY, UC, US); Little Lake Valley 2.5 mi. SE of Willits, *Wiggins & Ferris 10183* (CAS, RM, TEX, WS, WTU). Monterey Co., hill near Monterey, 13 June 1861, *Brewer 704* (UC, US). Napa Co., Knoxville, 8 May 1903, *Baker 3081* (F, GH, LL, MO, NY, UC); 5 mi. S of Calistoga, 12 Apr. 1924, *Heller 13837* (CAS, F, MO, NY, US). San Benito Co., Aromas, *Hickman* 1915 (CAS, GH, US). San Luis Obispo Co., along old road to Pozo, 17 May 1928, *Eastwood 15140* (CAS, UC); San Luis Obispo, 9 May 1882, *Jones 2660* (CAS, MO, NY, PH, RM, UC). San Mateo Co., Crystal Springs Lake, May 1903, *Elmer 4824* (ARIZ, CAS, MO, NY, OSC, UC, US, WS); Crystal Springs Lake, 1 May 1902, *Greene 685* (CAS, GH, LL, MO, NY, UC, US, WTU); Mt. Hamilton, June 1903, *Elmer 5023* (ARIZ, CAS, MO, NY, UC, WS); Smith Creek, foot of Mt. Hamilton, 10 May 1907, *Heller 8518* (CAS, GH, F, MO, NY, PH, UC, US, WTU); trail to Pine Ridge, N of Madrone Springs, 29 May 1895, *Smith 4075* (GH, OSC, RM, TEX). Santa Cruz Co., Glenwood, *Davis* 1907 (CAS, GH, RM, UC, US); Bear Creek Road about 3 mi. E of Boulder Creek, 18 May 1946, *Ferris 11130* (CAS, GH, RM, TEX, UT, WS). Sonoma Co., between Santa Rosa and Agua Caliente, 22 Apr. 1902, *Heller & Brown 5343* (CAS, COLO, GH, MO, NY, RM, US); 6.8 mi. E of Santa Rosa on road to Calistoga, 30 Apr. 1949, *Wiggins 12058* (CAS, UC, WTU).

This is the more commonly encountered, more variable taxon of the *Thermopsis californica* complex. It is distinguished from both *T. californica* var. *semota* and *T. californica* var. *argentata* by its larger habit, broader stipules and bracts, and sparsely to densely tomentose vestiture.

Brewer & Watson (1880) correctly noted that *Thermopsis macrophylla* is distinct from *T. californica*. Nevertheless, most workers have treated these taxa as synonymous with the earlier name, *Thermopsis macrophylla*. We view *T. macrophylla*, like Brewer & Watson, as a localized endemic that is restricted to the Santa Ynez Mountains near Santa Barbara, California. Collections of *Thermopsis californica* are not sympatric and do not intergrade with *T. macrophylla*. Isely (1981), who treated *T. californica* var. *californica* within his concept of *T. macrophylla* var. *macrophylla*, perceived "a cline towards [*T. macrophylla*] var. *venosa* [= *T. gracilis* in the present treatment] that characteristically has spreading and (comparatively) narrow fruits." This statement was qualified by the remark that "few specimens possess mature pods." Examination of many diverse specimens from northern California shows that the geographical hiatus shown by Isely in mapping the two taxa is real, and that the few collections of his *T. macrophylla* var. *macrophylla* that he maps within the range of *T. gracilis* (of the present treatment) are mostly nonfruiting forms of *T. gracilis* that are otherwise superficially similar to *T. macrophylla* var. *macrophylla* (sensu Isely). We do not see any evidence of clinal intergradation between these two taxa, nor do they co-occur, as suggested in Isely's treatment.

1c. Thermopsis californica var. **semota** (Jepson) C. J. Chen & B. Turner, comb. nov. Basionym: *Thermopsis macrophylla* Hook. & Arn. var. *semota* Jepson, Fl. Calif. 2: 245. 1936. *Thermopsis macrophylla* Hook. & Arn. subsp. *semota* (Jepson) Beauchamp, Phytologia 59: 439. 1986. TYPE: U.S.A. California: San Diego Co., Spencer Valley, vicinity of Julian, *Alderson* 1898 (holotype, UC).

Plants 3–5(–6) dm tall, densely silvery tomentose; branches moderately to strongly zigzagged. Leaflets elliptic to narrowly elliptic, 3–6.5(–7.5) cm long, 1.2–3.5(–3.8) cm wide, acute to obtuse with a short mucro; petioles 1–2 cm long; stipules ovate to lanceolate, 1.5–5.5 cm long, 0.7–2.4 cm wide, cuneate to cordate. Racemes 7–20(–30) cm long, with 10–30 flowers; peduncles 2–6(–9) cm long; bracts ovate to nearly lanceolate, 6–11 mm long, 3.5–6 mm wide. Calyx 5–8(–9) mm long, 5–8 mm wide at the limb, lobes 3–5 mm long; banner shallowly emarginate and short mucronate; wing and keel petals asymmetrically oblong-elliptic; ovules 5–7. Pods 2–4 cm long, 0.6–0.7 cm wide. Seeds 1–2 (fully matured not seen).

Distribution and ecology (Fig. 1). Interior portions of San Diego Co., California, grassy oak woodlands, 1000–1500 m; flowering April–June.

Representative specimens examined. U.S.A. **California:** San Diego Co., 1.7 mi. NW of Julian, 5 Apr. 1957, *Bacigalupi et al. 5799* (JEPS, RM, WTU); near Julian, *Epling* 1932 (CAS, NY, POM, UC); Cuyamaca Reservoir, 5 June 1946, *Fiker 3576* (RM, UC, WS); Julian, Cuyamaca Mts., 28 May 1899, *Hall 1205* (CAS, NY, UC); vicinity of Santa Ysabel, *Henshaw* 1893 (US);

Laguna Mts., 25 June 1924, *Munz 8377* (GH, NY, POM); Pine Hills, 1 June 1917, *Spencer 504* (GH, NY, POM, UC); Ramona, head of Cedar Creek, 27 Mar. 1934, *Wieslander 447* (UC).

Isely (1981) treated this taxon as a localized variety within his concept of *Thermopsis macrophylla*. We agree with his circumscription. Larisey (1940) inexplicably omitted the taxon from her treatment.

2. **Thermopsis divaricarpa** Nelson, Bot. Gaz. 25: 275. 1898. *Thermopsis rhombifolia* var. *divaricarpa* (Nelson) Isely, Brittonia 30: 470. 1978. TYPE: U.S.A. Wyoming: Albany Co., Johnson's ranch, Big Laramie River, 8 Aug. 1897, *A. Nelson 3903* (lectotype, selected here, RM; isolectotypes, GH, NY [dated 7 Aug. 1897], RM).

Thermopsis pinetorum E. Greene, Pittonia 4: 138. 1900. TYPE: U.S.A. Colorado: Saguache Co., below Marshall Pass, *Greene* 1896 (lectotype, selected here, ND; isolectotype, ND).

Two different collections of *Thermopsis divaricarpa*, *E. Nelson 3424* (Pole Creek, 22 July 1897) and *A. Nelson 3903*, were designated as "type specimens" by A. Nelson, without indication of the holotype. Isely (1978) designated *Nelson 3903* as the "holotype"; he should have designated this as a lectotype.

In his protologue for *Thermopsis pinetorum*, Greene cited collections made by himself "in fruit, below Marshall Pass," 4 Sep. 1896 and collections by C. F. Baker at Los Pinos (which is near Bayfield in La Plata Co.), 23 May 1899, in flower. The latter collections appear to belong to *Thermopsis montana*. The former is selected as the lectotype since mature fruits best serve to distinguish between the taxa concerned.

Plants delicate, 3–6(–9) dm tall, glabrate or puberulent; stems slender, erect, clustered, moderately branched, arising from a thick woody rootstock or rhizomes; branches ascending at 20–35°, moderately to strongly zigzagged. Leaflets elliptic to narrowly elliptic or rhombic, 3–7 cm long, 0.5–2.5 cm wide, acute to obtuse, glabrate to puberulent, lateral veins 7–10 pairs, conspicuously netveined beneath; petioles 1–2.5 cm long; stipules persistent, ovate to narrowly elliptic, 2–3.5(–4) cm long, 0.7–3 cm wide, cuneate to cordate, acute. Racemes 7–15 cm long, with 5–15 flowers, usually in whorls of 2–4; peduncles 3–5 cm long; pedicels 5–8 mm long, glabrate to puberulent; bracts deciduous, ovate to lanceolate, 7–14 mm long, 3–5 mm wide. Flowers 2.5–2.9 cm long; calyx 8–11 mm long, 6–8 mm wide at the limb, lobes 2–5 mm long, as long as or shorter than tube; wing and keel petals elliptic to asymmetrically oblong-elliptic; ovary appressed pubescent; ovules 10–18. Pods straight to arcuate to ca. 45°, divergent, 6.5–9 cm long, 0.6–0.8 cm wide, inconspicuously appressed pubescent. Seeds (6–)10–14, brown-black, elliptic with a rostrum, 4–5 mm long, 2–2.5 mm wide. Chromosome number, $2n = 36$.

Distribution and ecology (Fig. 2). South-central Wyoming (mainly Albany Co.) southeastward through the front range of the Rocky Mountains to northeasternmost New Mexico, mostly pine or spruce forests, usually along streams or in moist open areas, 2000–3000 m; flowering (April–)May–June(–July).

Representative specimens examined. U.S.A. **Colorado:** Alamosa Co., near S entrance of Great Sand Dunes National Monument, 18 May 1969, *Dennam 2950* (TENN). Boulder Co., Boulder, 21 Aug. 1884, *Letterman 141* (MO, US); plains and foothills near Boulder, July 1902, *Tweedy 5158* (NY, RM). Chaffee Co., Salida, 18 May 1925, *Nelson 10495* (NY); Salida, 7–8 Oct. 1918, *Eggleston 15019* (US). Clear Creek Co., Idaho Springs, rocky hillsides, 15 May 1916, *Clokey 2676* (RM, UC); Chicago Creek, 11 July 1942, *Ehlers 8398* (COLO, TEX); Empire, 2,576 m, 15–25 July 1903, *Tweedy 5652* (NY, RM). Costilla Co., mountain near La Veta Pass, 20 June 1900, *Rydberg & Vreeland 5935* (NY). Custer Co., North Creek Campground, 30 May 1954, *Douglass 58* (COLO); Sangre de Cristo Creek, 2 July 1900, *Rydberg & Vreeland 5933* (NY, RM). Douglas Co., along Colorado Hwy. 67, 8.3 mi. N of junction of Colorado Hwy. 67 and County Road 126, 18 May 1987, *Falb & Miercort 113* (RM). El Paso Co., Colorado Springs, *Jones* 1879 (ARIZ, NY, US); near Palmer Lake, 21 June 1936, *Rollins 1187* (GH, MO, ND, NY); Garden of the Gods, *Schallert* 1943 (F, NY, PH, WS). Fremont Co., near Hillside, 4 June 1949, *Gates 22053* (TEX). Garfield Co., White River, Grizzly Creek, 26 June 1932, *Ware 24* (RM); 38.8 mi. S of junction Colorado Hwy. 64 on Colorado Hwy. 139, 14 June 1971, *Wofford 1-77* (TENN). Gilpin Co., near summit of Black Hawk Pass, *Alston* 1964 (TEX); Tolland, *Overholts* 1913 (MO, NY). Grand Co., Trail Ridge Road, 11.5 mi. N of Grand Lake, 21 July 1961, *Douglass 320* (TEX); Hot Sulphur Springs, 30 May 1940, *Pohl 1954* (PH). Huerfano Co., 8 mi. SW of Cuchara, Bear Lake Camp, 4 Aug. 1970, *Stephens & Brooks 42675* (NY, UC); Erwind Canyon, W of Walsenburg, 14 June 1941, *A. & R. A. Nelson 4595* (RM). Jackson Co., Gould Ranger Station, 23 Sep. 1944, *Ginter 891* (RM). Jefferson Co., Vernon Canyon, 20 June 1921, *Bethel & Clokey 4186* (CAS, COLO, F, MO, NY, PH, POM, RM, UC, US); near Golden, Guy Hill, 2 June 1938, *Ehlers 6850* (ARIZ, GH, NCU, ND, PH); ca. 11 mi. W of Littleton, 20 May 1967, *Turner 5637* (CAS, RM, TEX). Lake Co., Everett, 7 May 1919, *Clokey 3588* (CAS, F, GH, MO, POM, RM, TEX, US). Larimer Co., Estes Park, May 1895, *Baker 2581* (COLO, MO, NCU, WS). Las Animas Co., 11 mi. N of Stonewall, 26 May 1968, *Turner 5772* (TEX). Mesa Co., 13 Aug. 1981, *Siplivinsky 1961*

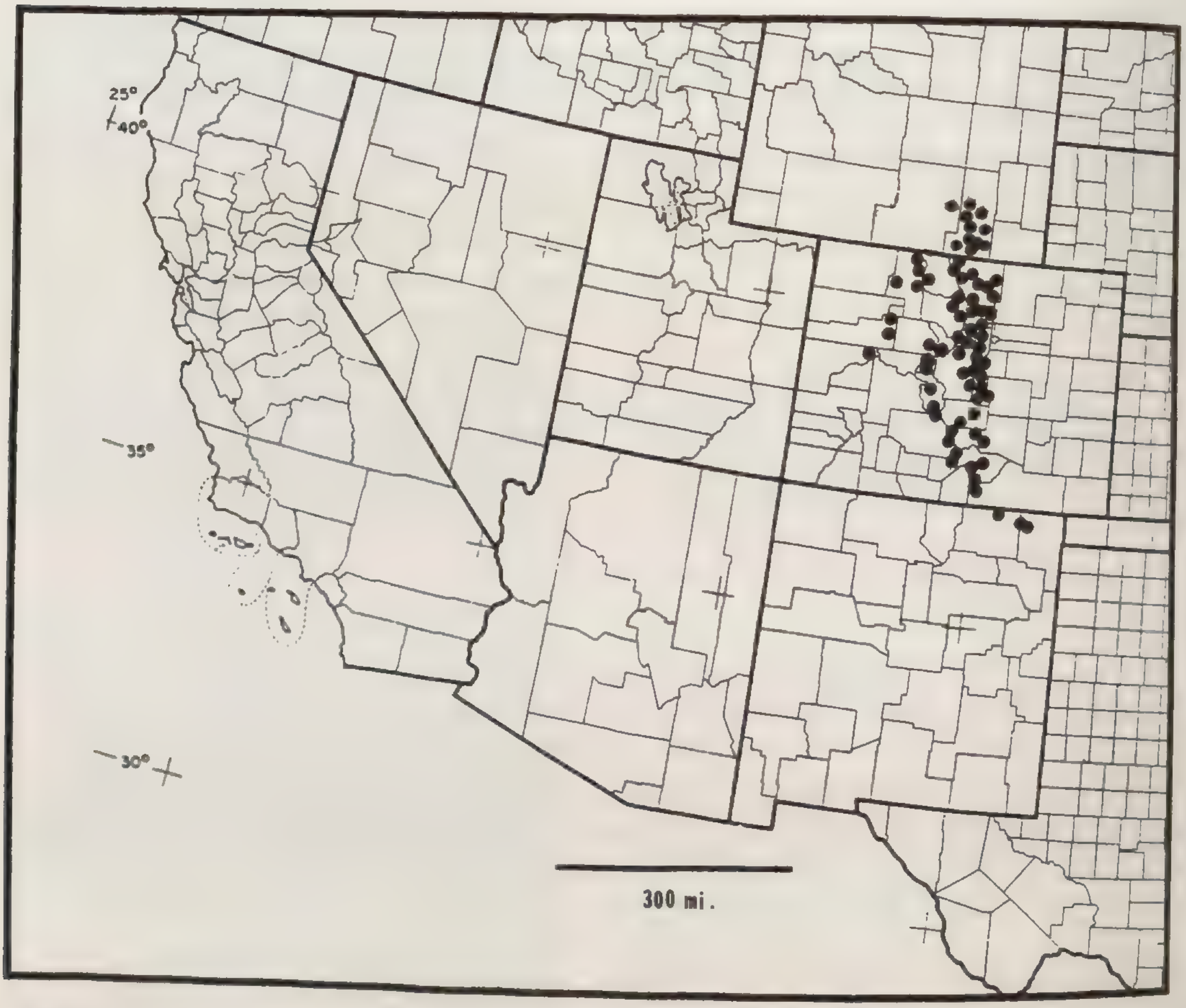

FIGURE 2. Distribution of *Thermopsis divaricarpa*.

(COLO). Park Co., Pine Junction to Wandcrest Park, 27 June 1971, *Kathleen & Shea 65* (MO); near Jefferson, Michigan Creek drainage, 16 July 1960, *Walter 369* (COLO). Pueblo Co., near Beulah, 6 June 1908, *Robbins 4991* (COLO); W of Pueblo, 8 May 1908, *Robbins 4991* (COLO). Routt Co., Elkhead Mts., 10 July 1988, *Flock 2004* (COLO, RM); Anita Peak, 3 Aug. 1903, *Goodding 779* (CAS, COLO, GH, MO, NY, PH, RM, UC, US). Saguache Co., Marshall Pass, 19 July 1901, *Baker 485* (F, MO, NY, RM, UC, US); 8 mi. E of Marshall Pass, 27 May 1968, *Turner 5776* (TEX). Summit Co., near Breckenridge, *Mackenzie 256* (MO, NY, RM, UC); near Bear River, 30 June 1926, *Payson 4833* (GH). Teller Co., S side of Lower Twin Rocks Road, 10 June 1987, *Barzee et al. 717* (COLO); 6 mi. NNW of Woodland Park, *Devender & Kearns* 1977 (ARIZ). **New Mexico:** Colfax Co., Cimarron Pass, 28 May 1934, *McKelvey 2405* (GH); Raton, 10 June 1887, *Evans 59* (NY). Union Co., Sierra Grande, 19 June 1911, *Standley 6140* (US); 7 mi. S of Des Moines, 14 May 1974, *Stephens 75588* (NY). **Wyoming:** Albany Co., Vedauwoo Hills E of Laramie, 13 June 1940, *Cain 65* (MO, TENN); Little Laramie River, 15 June 1901, *Goodding 10* (CAS, F, GH, MO, NY, POM, RM, UC, US, UT); Rock River, 30 June 1914, *Macbride 2403* (RM, WS); Big Laramie River, 5 July 1900, *Nelson 271* (GH, NY, RM); Sand Creek, 2 June 1900, *Nelson 7031* (CAS, COLO, GH, MO, NY, POM, RM, UC, US); Mandel, 24 July 1903, *Nelson 8910* (COLO, GH, MO, NY, UC); Fish Creek, 4 July 1917, *Nelson 9784* (GH, MO, RM, TENN, UC); Pole Mt. region, 6 July 1943, *Porter 3245* (CAS, GH, MO, NY, UC, US, WTU); Crow Creek, Laramie Hills, 11 July 1935, *Rollins 977* (GH, MO, NY, WS); Laramie River near Laramie, 16 June 1935, *Williams 2214* (GH, MO, UC, US); near Crow Creek, Laramie Mts., 20 June 1935, *Williams 2236* (GH, MO, UC, WS). Carbon Co., McFadden, in Medicine Bow Mts., 13 June 1972, *Jones 1085* (MO).

Isely (1981) treated this taxon within his broad concept of *Thermopsis rhombifolia*, noting that it stands morphologically and geographically somewhat between *T. rhombifolia* and *T. montana*, which it does. Nevertheless, we have retained *T. divaricarpa* as a distinct species.

We have found that *T. rhombifolia*, *T. divaricarpa*, and *T. montana* are clearly distinct throughout most of their ranges and do not appear to intergrade as do the varieties in the *Thermopsis montana* complex. Indeed, in Colorado where the several taxa are partially sympatric, *T. rhombifolia*

occurs mostly at lower elevations in deeper and drier alluvial soils, *T. divaricarpa* at mid-elevations in mesophytic habitats, and *T. montana* at higher, subalpine elevations.

It is true, however, that occasional intermediates between *Thermopsis divaricarpa* and *T. rhombifolia* occur, but we view such variation as derived from relatively isolated hybridization events. Such "hybridized" populations occur in Albany County, Wyoming, and probably occasioned the description of *T. arenosa*, which appears to combine some of the features of *T. divaricarpa* in the genetic backdrop of *T. rhombifolia*. Likewise, in Colorado at Marshall Pass along the Saguache-Chaffee county line, *T. montana* and *T. divaricarpa* occur in close proximity and there has apparently been some gene exchange between the two. The variants from this region have the general habit of *T. divaricarpa*, but the ascending pods approach those of *T. montana*. The form may have precipitated the description of *T. pinetorum*. The third author visited the general area of the type locality of *T. pinetorum* in May 1968 (*Turner 5776*, TEX) and again in July 1991, and was impressed by the populational variation in that vicinity, especially along the eastern slopes leading to Marshall Pass. But such morphological aberrations are mere wrinkles in the broad distributional fabric of *T. rhombifolia*, *T. divaricarpa*, and *T. montana* and do not make a case for their taxonomic submergence. If it were so, then many distinct species among the closely related genus *Baptisia* would be merged, for occasional or even rampant hybridization is the rule when species of these taxa occur together (under disturbance). Indeed, interspecific hybridization between the closely related taxa *T. rhombifolia*, *T. divaricarpa*, and *T. montana* is apparently much less common than among the more distantly related (among themselves) species, *Baptisia leucophaea*, *B. sphaerocarpa*, and *B. leucantha* (Alston & Turner, 1963).

It is indeed likely, however, that *T. divaricarpa* had an amphiploid origin from *T. rhombifolia* and *T. montana*. So far as is known, *T. divaricarpa* is tetraploid with $2n = 36$ and has morphological features somewhat intermediate between the diploid species *T. rhombifolia* and *T. montana*, both with $2n = 18$. Perhaps the formation of amphiploids was preceded by some gene exchange between *T. rhombifolia* and *T. montana* at the diploid level. The present ranges suggest that extensive introgression between these taxa was not likely. It should prove interesting to test these various hypotheses using molecular characters. Regardless, we believe that the taxonomic community is best served at the present time with the taxonomic treatment adopted here, this being clearly depicted to those working with living populations in the field.

Isely (1981) maps, but does not cite, at least five collections of *Thermopsis divaricarpa* (as *T. montana* var. *divaricarpa*) from western Montana, but we believe these to be misidentified elements of *T. montana* var. *montana* or *T. rhombifolia*. In addition, he maps at least a few collections of *T. divaricarpa* from northeastern Wyoming that we believe to be misidentified elements of fairly typical *T. rhombifolia*.

Isely (1981) included *Thermopsis pinetorum* as a synonym of his *T. rhombifolia* var. *montana* but examination of type material, as noted above, shows that the name apparently was typified by mixed collections; the lectotype belongs to his variety *divaricarpa*.

Nelson, in his original description of *T. divaricarpa*, provided excellent illustrations of the fruiting branches of *T. montana*, *T. divaricarpa*, and *T. rhombifolia*, along with a seemingly intermediate branch between *T. rhombifolia* and *T. divaricarpa* that he named *T. arenosa*. Although we relegate the latter name to synonymy under "typical" *T. rhombifolia*, in truth, *T. arenosa* is probably a hybrid or introgressed individual between *T. rhombifolia* and *T. divaricarpa*.

3. **Thermopsis fraxinifolia** (Nutt. ex Torrey & A. Gray) M. Curtis, Amer. J. Sci. 44: 81. 1843. *Baptisia fraxinifolia* Nutt. ex Torrey & A. Gray, Fl. N. Amer. 1: 387. 1840. *Thermopsis mollis* var. *fraxinifolia* (Nutt. ex Torrey & A. Gray) Isely, Brittonia 30: 469. 1978. TYPE: U.S.A. North Carolina: Burke Co., Table Mountain ("Catawba Ridge" of Nuttall; Graustein, 1967), *Nuttall* 1816 (holotype, PH; possible isotypes, GH, NY).

There remains a problem with the correct author citation for *Thermopsis fraxinifolia*. This is summarized by Wilbur (1963) who contended that the correct citation should be *T. fraxinifolia* M. Curtis ex A. Gray (published in 1848). Isely (1978) accepted this, but he subsequently took up the citation *T. fraxinifolia* Nutt. ex Torrey & A. Gray (1840) (Isely, 1981). We believe this to be the preferred citation because Torrey & Gray (1840) cited a Nuttall specimen and quoted a description provided by him in their discussion of *T. fraxinifolia*. Contrary to Wilbur's observation, the Nuttall name was not rejected by Torrey & Gray. They merely noted that the species had not fallen under their observation and that it was "uncertain whether it

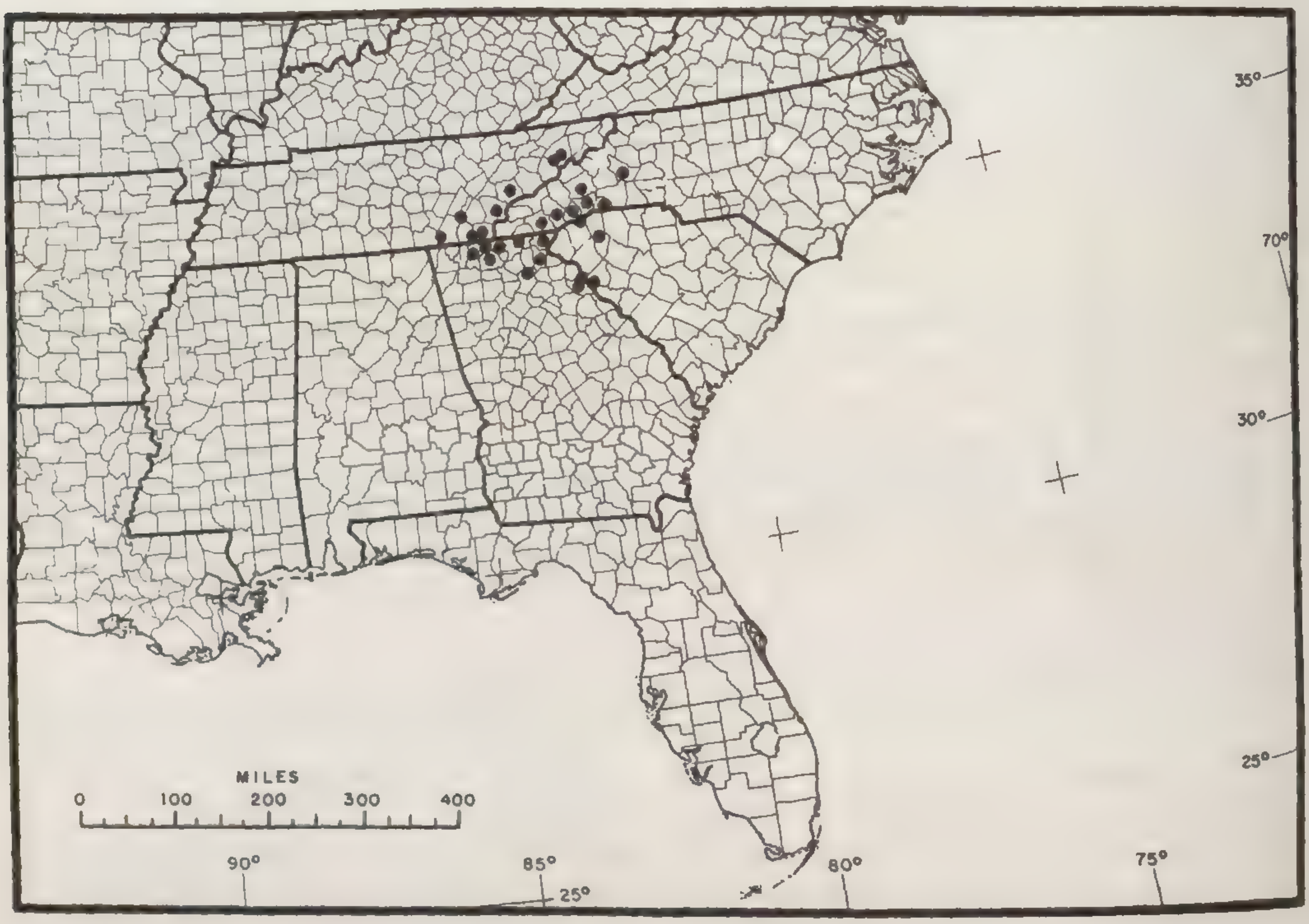

FIGURE 3. Distribution of *Thermopsis fraxinifolia*.

[*T. fraxinifolia*] be distinct from some of the species described above." We do not view this as a rejection of the name, but rather a form of abeyance.

Plants delicate, 5–10 dm tall, glabrate to sparsely puberulent; stems slender, erect, clustered, well-branched, arising from a single woody rootstock; branches spreading at 45–80°, strongly zigzagged. Leaflets elliptic, 4.5–8 cm long, 2–3.5 cm wide, acute to acuminate, glabrous to very sparsely puberulent, lateral veins 9–12 pairs, very conspicuously net-veined beneath; petioles 1.6–3 cm long; stipules sometimes persistent, lanceolate to narrowly ovate, 1–3.5 cm long, 0.3–0.8 cm wide, cuneate, acuminate. Racemes terminal or lateral, 12–25 cm long, with 7–25 flowers, scattered; peduncles 2.5–5.5 cm long; pedicels 7–17 mm long, glabrate; bracts persistent, lanceolate, 8–12 mm long, 1–3 mm wide. Flowers 1.6–1.9 cm long; calyx 7–9 mm long, 4–5 mm wide at the limb, lobes 2–3 mm long, much shorter than tube; wings elliptic to asymmetrically oblong-elliptic; keel asymmetrically oblong-elliptic; ovary appressed pubescent; ovules (6–)12–16. Pods straight, irregularly divergent, (3–)5.5–7.5 cm long, 0.3–0.5 cm wide, inconspicuously pubescent. Seeds (5–)10–15, brown, reniform with a very short rostrum, 4 mm long, 2.5 mm wide. Chromosome number, $2n = 18$.

Distribution and ecology (Fig. 3). Southernmost Appalachian Mountains in eastern Tennessee, western North Carolina and adjacent Georgia and South Carolina, rich woods, mostly upper hillslopes along streams and at lower elevations along floodplains, (300–)700–1600 m; flowering (April–)May–July.

Representative specimens examined. U.S.A. **Georgia:** Fannin Co., NE of Cisco and NW of Blue Ridge, along Jack's Trail and Jack's River, 6 June 1983, *Coile et al. 3610* (RM, TENN). Gilmer Co., near Stanley Gap, 7 June 1982, *Coile et al. 2844* (POM, TEX). Habersham Co., *Small* 1895 (ARIZ, F, NY). Hall Co., near Gainesville, *Huger* 1897 (NY). Murray Co., mountain slopes between Cohutta and Fort Mountains, 27 May 1935, *Duncan & Hardin 16468* (NCU). Oglethorpe Co., ca. 0.75 mi. S of the Georgia Hwy. 368 bridge over the Savannah River, 200 m, 7 June 1979, *Credle 863* (NCU); near bridge of Georgia Hwy. 72 on Savannah River, 10 June 1978, *Robert & Coile 1860* (NCU). Rabun Co., Rabun Bald, 1–4 June 1906, *House 2266* (US); Tallulah Falls, *Small* 1893 (F, NY). Towns Co., Young Harris, 10 July 1908, *Howell 390* (MO, US). **North Carolina:** Buncombe Co., Black Mountain, 12 Aug. 1905, *Biltmore Herbarium 11214* (F, GH, MO, NY, US); Asheville, *Kraus* 1925 (MO, POM, UC). Burke Co., vicinity of Table Rock Mt., 2 Aug. 1890, *Heller 27* (F, MO, NY, POM, UC). Henderson Co., Flat Rock, *Gibbes* 1854 &

1858 (NY). Macon Co., 1.4 mi. N of the Georgia state line on North Carolina Route 28, 1 June 1975, *Wood & Boufford 1389* (A); 2.1 mi. N of the Georgia state line on North Carolina Route 28, 1 June 1975, *Boufford 16075* (MO). Polk Co., Pony Mt., *Townsend* 1897 (US). Transylvania Co., Whitewater River, just above Upper Falls, 7 June 1951, *Godfrey 51298* (MO). Yancey Co., Mt. Mitchell, *Rhoades* 1932 (GH, PH, RM); E of Mt. Mitchell, exactly 2.3 mi. SW of Rough Ridge Tunnel, 30 June 1970, *Turner 6076* (ARIZ, CAS, F, MO, NY, TEX). **South Carolina:** Abbeville Co., 3 mi. SW of Calhoun Falls, near Savannah River, 13 May 1957, *Radford 22768* (NCU, UC). Greenville Co., Caesars Head, *Smith* 1881 (F, GH, MO, NY, US). Oconee Co., *Boynton* 1889 (CAS). Pickens Co., 0.7 mi. off U.S. Hwy. 178 on Sassafras Mt. Road, 30 June 1970, *Turner 6075* (ARIZ, CAS, COLO, F, GH, MO, NCU, NY, RM, TEX, WTU). **Tennessee:** Blount Co., Chilhowee Mountain, 10.98 km SW of Tennessee Hwy. 73 on Foothills Parkway, 650 m, 26 May 1982, *Boufford & Spongberg 22881* (A, MO, NCU, POM, TEX). Greene Co., 2.3 road mi. S of Camp Creek School, just N of Horsehitch Gap, 10 June 1980, *Boom & Smith 547* (TENN); along Kennedy Cabin loop road, 11 June 1980, *Boom & Perkins 554* (TENN); mountain slope between Camp Creek and Paint Creek on Green Mt., 30 July 1950, *Shanks & Sharp 7455* (TENN). Hamilton Co., Lookout Mt., *Canby* 1869 (F, GH, MO, NCU, NY, PH, US). Monroe Co., Waucheesi Mt. on FR 126-C, 12 June 1978, *Whitten & Mescall 213* (TENN). Polk Co., Peavine Road, 5.8 road mi. SW of Ocoee No. 3 Powerhouse, 23 May 1980, *Boom 471* (TENN); Wolf Ridge, 25 June 1983, *Z. E. & J. B. Murrell 336* (TENN). **Cultivated:** Massachusetts, Botanical Garden of Cambridge, *Gray s.n.* (NY).

This species is partially sympatric with *Thermopsis mollis*, but in regions of overlap *T. fraxinifolia* usually occurs at higher elevations along the upper slopes of the mountainous ridges and hills of the Appalachians. *Thermopsis fraxinifolia* may also occur at lower elevations on alluvial deposits along at least some of the rivers in this region.

Thermopsis fraxinifolia can be distinguished from *T. mollis* by its more robust, more branching habit, lateral (as well as terminal) inflorescences, and longer pedicels. Furthermore, *Thermopsis mollis* propagates by extensive, vigorous rhizomes, which are absent in *T. fraxinifolia*. Both species were well known to Asa Gray, who personally collected *T. fraxinifolia* at its type locality and subsequently grew this at the botanical gardens at Harvard. According to Gray (1848b), *T. mollis* was also maintained in the Harvard Botanical Gardens at the same time. Living specimens of both were used to make the excellent illustrations of the two species that accompany his treatment of *Thermopsis* of the eastern United States.

As noted by Gray (1848b), Wilbur (1963), and Radford et al. (1968), *Thermopsis mollis* is mostly a piedmont species, distributed along the middle and western portions of North Carolina and adjacent states, occasionally extending into the mountains, where its range abuts that of *T. fraxinifolia*. Indeed, we do not know of any specific sites where the two have been collected together, nor do we perceive a large set of intermediate plants in regions of near contact (or elsewhere) that might justify their recognition as regional variants of a single species, as treated by Isely (1981). His distribution maps of both taxa are fairly accurate, although these are difficult to evaluate since he did not cite specimens documenting the distributions shown.

Isely (1981) did map a number of specimens from easternmost Tennessee that appear to be anomalous. These are morphologically somewhere between *Thermopsis mollis* and *T. fraxinifolia* and were designated "*T. mollis* var.?" on Isely's map. We believe that many of these may be derivatives of hybridization between *T. mollis* and *T. fraxinifolia*. The species occur in close proximity in this region and the intermediates have the habit of *T. mollis* but the inflorescence pattern and general habitat preference of *T. fraxinifolia*. Both *T. mollis* and *T. fraxinifolia* have been collected on Lookout Mountain, Hamilton Co., Tennessee, as have several of the putative hybrid intermediates (e.g., *Churchill* 1911, TENN; *Canby* 1869, GH, MO, NCU, NY, PH, US).

More detailed field investigations may show that the hypothetical hybrids may, in fact, be part of a more widespread, highly variable taxon derived from ancestral hybridization between *Thermopsis mollis* and *T. fraxinifolia*. This is inferred from recent collections by Boufford & Spongberg from Blount Co., Tennessee (*22881*, GH, MO, NCU, TEX), and by Whitten from Monroe Co., Tennessee (*213*, TENN), which seem to reveal stabilized populations of intermediate morphology in this area. Some of the characters in at least a few of these plants are unique within the American taxa of *Thermopsis*. For example, the Blount County specimens cited above have short, squat pods with distinct gynophores, much as occurs in some of the Asian species. On the present information, however, it is more sensible to include such plants within a variable *T. fraxinifolia* than to accord these varietal status.

4. **Thermopsis gracilis** Howell, Erythea 1: 109. 1893. TYPE: U.S.A. Oregon: Josephine Co., "Mountains near Waldo," 5 July 1887, *T. J. Howell 669* (holotype, ORE; isotypes, CAS, GH).

Thermopsis venosa Eastw., Bull. Torrey Bot. Club 32: 198. 1905. *Thermopsis gracilis* var. *venosa* (Eastw.) Jepson, Man. Fl. Pl. Calif. 515. 1925. *Thermopsis*

montana var. *venosa* (Eastw.) Jepson, Fl. Calif. 2: 245. 1936. *Thermopsis macrophylla* var. *venosa* (Eastw.) Isely, Brittonia 30: 469. 1978. TYPE: U.S.A. California: Shasta (or Trinity) Co., "Lewiston Trail near the summit that divides Trinity from Shasta County, California," *Eastwood* 1901 (holotype, CAS).

Thermopsis subglabra L. Henderson, Rhodora 32: 26. 1930. TYPE: U.S.A. Oregon: Lane Co., "Shady woods of Culp Creek, near base of Bohemia Mt. Divide, between Lane and Douglas Counties, Oregon," 1600 m, 2 May 1926, *J. R. Patterson 9959* (lectotype, selected here, ORE).

In his protologue for *Thermopsis gracilis*, Howell did not mention a specific type but rather noted the species to occur in "Mountains of southwestern Oregon, from the sources of the Willamette, to northern California," which suggests that he knew the plant from a number of collections. Actually, there is only a single sheet at ORE that could have served as the voucher for *Thermopsis gracilis*. L. A. Vorobik, by annotation, selected this as the holotype. A purist might have called this a lectotype.

Plants robust, 3–8 dm tall, glabrous to sparsely villous; stems slender, erect, single or clustered, well-branched, arising from a woody rootstock or rhizomes, branches spreading at 30–70°, moderately to strongly zigzagged. Leaflets elliptic to obovate or rhombic, 3–6(–8) cm long, 2–3.2 cm wide, acute, obtuse, or emarginate, glabrous, lateral veins 6–9 pairs, very conspicuously net-veined beneath; petioles 2.5–4(–5) cm long; stipules persistent, asymmetrically ovate-elliptic, 2.5–3.5 cm long, 1.5–3 cm wide, cuneate to cordate, acuminate. Racemes 12–20(–30) cm long, with 7–30 flowers, scattered; peduncles 4–9(–11) cm long; pedicels 6–16 mm long, glabrous to sparsely villous; bracts semipersistent, ovate, 6–8 mm long, 3–5 mm wide. Flowers 2–2.3 cm long; calyx 8–10 mm long, 7–8 mm wide at the limb, lobes 2–3 mm long, much shorter than tube; wings elliptic; keel asymmetrically oblong-elliptic; ovary sparsely villous; ovules 9–14. Pods straight, irregularly divergent, 3–6 cm long, 0.4–0.6 cm wide, inconspicuously pubescent. Seeds 2–8, tan, oblong with a short rostrum, 3–4 mm long, 2 mm wide. Chromosome number, $2n = 36$.

Distribution and ecology (Figs. 1, 4). Northwestern California and adjacent Oregon, mesophytic lower montane evergreen forests, mostly 100–1200 m; flowering (April–)May–June.

Representative specimens examined. U.S.A. **California:** Del Norte Co., Siskiyou lowlands near Gasquet, 22 Apr. 1939, *Meola 69* (OSC, UC); N side of Middle Fork of Smith River on Old Gasquet Toll Road, 1 June 1935, *Parks & Tracy 11227* (CAS, GH, UC, WTU); 2 mi. S of Gasquet on French Hill Road, 1 June 1968, *Turner 5801* (CAS, GH, NY, TEX). Humboldt Co., French Camp Ridge, in chaparral, 6 Aug. 1933, *Tracy 12955* (UC, WTU); Willow Creek Canyon, along Trinity Hwy., rocky point at Ruby Creek, 31 May 1937, *Tracy 15326* (UC, WTU). Shasta Co., between La Moine and Williams Ranch, 19 June 1919, *Heller 13250* (CAS, GH, MO, NY, PH, UC, WTU); McCloud Fork, 24 Apr. 1913, *Smith 110* (GH, MO, NY). Siskiyou Co., Dunsmuir, 23 July 1912, *Eastwood 1319* (CAS, GH, MO, NY, US); ca. 2 mi. S of Shasta Springs, on the old McCloud Road, 2 June 1968, *Turner 5807* (TEX). Trinity Co., E of Weaver Creek, 21 May 1914, *Yates 7-72* (RM, US). **Oregon:** Benton Co., Mary's Peak Road, ca. 10 mi. SW of Corvallis, *Mills* 1973 (UT); Philomath, 23 May 1925, *Stason 2399* (UC). Coos Co., 3 km NE of Remote, 7 May 1980, *Sundberg 994* (OSC). Curry Co., 2 mi. SW of turn-off from road to Agness along road to Iron Mt., 16 June 1956, *Balls & Lenz 21697* (CAS, NY, POM, RM, UC, UT, WS); Mt. Emily, lower chaparral belt, 10 Aug. 1921, *Jepson & Tracy 5909* (TEX, UC). Douglas Co., Dog Creek drainage of N. Umpqua River upstream from Steamboat River, above Limpy Rock, 19 June 1976, *Chambers 4223* (CAS, NCU, POM, WTU); 10 mi. from West Fork, 27 June 1917, *Peck 7255* (F, OSC). Jackson Co., Grave Creek near Winarr, 14 May 1889, *Hammond 74* (MO). Josephine Co., summit of the lower Siskiyou Mts. especially N slopes, 3 July 1902, *Cusick 2927* (F, GH, MO, NY, OSC, POM, UC, US, WS); Waldo, July 1894, *Howell 1495* (COLO, MO, NY, ORE, OSC, PH, UC, US, WS, WTU); Onion Mt. Road, 11 May 1956, *Steward 7059* (CAS, MO, NCU, OSC, PH, POM, TENN); Sexton Mt., 9 Apr. 1934, *Thompson 10209* (CAS, NY, POM, WYU). Lane Co., Spencer's Butte, 4 mi. S of

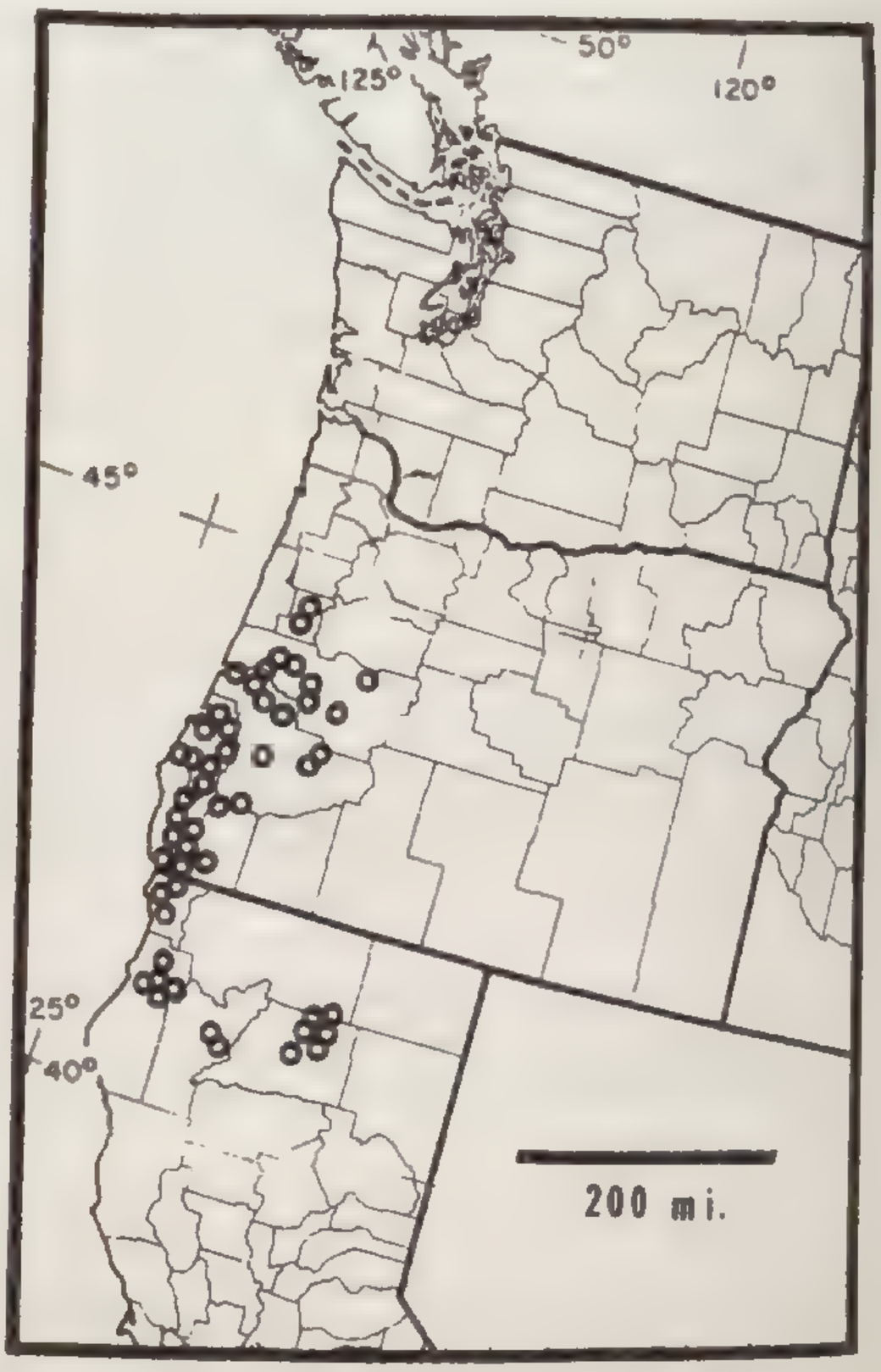

FIGURE 4. Distribution of *Thermopsis gracilis*.

Eugene, 5 May 1946, *Baker 2791* (ARIZ, CAS, MO, NY, OSC, WTU); near Cottage Grove, Lorane Road, 17 May 1931, *Henderson 13574* (PH). Lincoln Co., Alsea Mts., *Lammi* 1939 (OSC). Polk Co., 2 mi. W of Grand Ronde, *Brehm* 1967 (TEX).

This species is readily distinguished from the closely allopatric *Thermopsis californica* and *T. montana* by its divergent pods, spreading branches, and glabrous to sparsely pubescent foliage. It is most closely related to *T. robusta*, which also has divergent pods but which differs in its very robust habit, densely pilose vestiture, and longer calyx lobes. Larisey (1940) maintained *Thermopsis venosa* as a variety of *T. gracilis*, but Isely (1981) treated both names as synonyms under *T. macrophylla* var. *venosa*. If Isely's treatment is accepted, the correct taxon name under the existing nomenclatural code would be *Thermopsis macrophylla* var. *gracilis*, since that combination was validated with the erection of *T. gracilis* var. *venosa*. Regardless, we feel that *T. gracilis* is clearly distinct from *T. macrophylla*, as discussed in detail under the latter.

5. **Thermopsis macrophylla** Hook. & Arn., Bot. Beechey Voy. 329. 1840. TYPE: U.S.A. California: Santa Barbara Co.?, spring of 1833?, probably Santa Ynez Mt., near Santa Barbara, *Douglas s.n.* (holotype, K; photo of holotype, POM, UC; isotype, GH).

Thermopsis macrophylla var. *agnina* J. Howell, Leafl. W. Bot. 8: 158. 1957. TYPE: U.S.A. California: Santa Barbara Co., Camino Cielo, ca. 1 mi. W of Santa Ynez Peak. ca. 1060 m, *H. M. Pollard* 1955, plant B, 2 sheets (lectotype, selected here, CAS; isolectotypes, CAS [2 sheets plant A], US [3 sheets]).

Many workers have pondered over the type locality of *Thermopsis macrophylla*, equating *Thermopsis macrophylla* with *Thermopsis californica* S. Watson, but examination of type material and knowledge of the variation of *Thermopsis californica* throughout its range strongly suggest that *Thermopsis macrophylla* was originally collected in the Santa Ynez Mountains near Santa Barbara. Douglas resided for a time in Monterey, Santa Cruz County, California, from where he made several overland visits to Santa Barbara Mission. Eastwood, as noted by Howell (1957), thought she might have rediscovered the type locality of *Thermopsis macrophylla* in the Santa Cruz Mountains, Santa Cruz County, California, near Glenwood, but examination of this material (*Davis* 1907, CAS, GH, RM, UC, US) reveals these to be robust forms of otherwise typical *Thermopsis californica*. Howell also discussed the possible type locality of *Thermopsis macrophylla* in connection with his description of *T. macrophylla* var. *agnina*, suggesting a type locality for *T. macrophylla* near Aromas in San Benito County. But these, too, are merely large-leaved forms of otherwise typical *Thermopsis californica*. Type specimens of *Thermopsis macrophylla* match very closely those of *T. macrophylla* var. *agnina* and had Howell examined material of the Douglas collection we believe he would not have described the latter. No doubt much of the confusion regarding recognition of both *Thermopsis macrophylla* and *T. californica* is due to the fact that *T. macrophylla* is a relatively rare localized endemic. This has been confounded by the existence of *Thermopsis robusta*, a localized robust endemic with divergent pods, which is related to *T. gracilis* but is superficially similar to *T. macrophylla* in habit and vestiture. At least several workers who have recognized *Thermopsis macrophylla* as distinct from *T. californica* have treated both *T. macrophylla* and *T. robusta* as the same.

Plants robust, 12–23 dm tall, tomentose; stems thick, erect, solitary or few, moderately branched, from a woody rootstock, branches ascending at 45°, moderately zigzagged. Leaflets elliptic, 4–10 cm long, 2–5 cm wide, villous, acute, lateral veins 6–8 pairs, not conspicuously net-veined beneath; petioles 2–5(–7) cm long; stipules persistent, widely ovate, 3–9 cm long, 2–6 cm wide, amplexicaul to cordate, acuminate. Racemes 25–60 cm long, with 30–90 flowers, in whorls of 3–5; peduncles 8–15 cm long; pedicels 2.5–4 mm long, villous; bracts persistent, ovate to lanceolate, 8–10 mm long, 3–5 mm wide. Flowers 1.7–2.2 cm long; calyx 7–9 mm long, 7–8 mm wide at the limb, lobes 3–4 mm long, as long as or shorter than tube; wings elliptic; keel obovate; ovary velutinous; ovules 7–9. Pods straight, ascending, 3.5–5 cm long, 0.5–0.7 cm wide, villous. Seeds 5–7, brown-black, widely elliptic with a short rostrum, 4–5 mm long, 2.5–3.0 mm wide. Chromosome number, $2n = 18$.

Distribution and ecology (Fig. 1). Known only from the Santa Ynez Mountains, Santa Barbara Co., California, where it is locally common on the west side of Santa Ynez Peak near the summit, in sandy granitic soils, 1000–1400 m; flowering May–June.

Specimens examined. U.S.A. **California:** Los Angeles Co., Claremont, weed on the Rancho Santa Ana Botanic Garden grounds, "apparently introduced," 9 May 1991, *Ross 5047* (POM). Santa Barbara Co., S slope of Santa Ynez Peak, 1130 m, 11 May 1962, *Breedlove 2695* (CAS, POM); Santa Ynez Peak, *Fairfax* 1977 (RM); Santa Ynez Peak, ca. 4000 ft., *Pollard* 1956 (CAS,

TEX); in chaparral W of Santa Ynez Peak, 17 Oct. 1945, *Smith 1620* (POM); just W of Santa Ynez Peak, 12 May 1957, *Smith 5283* (POM); ca. 0.5 mi. due W of Santa Ynez Peak, 4 June 1968, *Turner 5820* (GH, NY, TEX); Santa Ynez Mts., along W Camino Cielo Road, 5.5 mi. E of intersection with Refugio Road, 3900 ft., 26 June 1992, *Junak 5022* (TEX); Santa Ynez Mts., along W Camino Cielo Road, 6.2 mi. E of intersection with Refugio Road, 4020 ft., 26 June 1992, *Junak 5020* (TEX).

The relationship of this localized endemic and its longtime confusion with *Thermopsis californica* is discussed in the above account of its typification. The early workers, mainly S. Watson, who possessed an isotype of *T. macrophylla*, maintained both *T. californica* and *T. macrophylla* as conceived in the present study. Subsequent workers, mostly Californian, confounded the two taxa. The taxa were not clarified by Larisey (1940), who treated both *T. californica* and *T. robusta* as synonymous with her *T. macrophylla* var. *macrophylla* (she ignored *T. macrophylla* var. *agnina*). In this Larisey was followed by Isely (1981) who also treated all of these as synonymous with his concept of *T. macrophylla* var. *macrophylla*. To our knowledge, Douglas made only two collections of *Thermopsis* in California, the type of *T. macrophylla* and a collection of *T. californica* var. *californica*. Torrey & Gray (1840) referred the latter to *T. macrophylla* var. *β*. This specimen (GH) is a fairly typical specimen of *T. californica*, presumably collected in the spring of 1833, perhaps in the vicinity of Monterey, California, to judge from its flowering state and vestiture.

6. Thermopsis mollis (Michaux) M. Curtis ex A. Gray, Mem. Amer. Acad. Arts n.s. 3: 47. 1848. *Podalyria mollis* Michaux, Fl. Bor.-Amer. 1: 264. 1803. *Baptisia mollis* (Michaux) Nutt., Gen. N. Amer. Pl. 1: 281. 1818. TYPE: U.S.A. North Carolina: Mecklenburg Co., vicinity of Mecklenburg, without date, *Michaux s.n.* (holotype, P not seen; probable isotype, PH).

Baptisia hugeri Small, Bull. Torrey Bot. Club 25: 139. 1898. *Thermopsis hugeri* (Small) Small, Fl. S.E. U.S. 596, 1331. 1903. TYPE: U.S.A. Georgia: Habersham Co., "northern slope on Mount Griffin," near Cornelia, *A. M. Huger* 1897 (holotype, NY; isotype, MO).

Plants delicate, 3–6 dm tall, sparsely appressed pubescent; stems slender, ascending or spreading, solitary or clustered, moderately branched, arising from extensive rhizomes; branches spreading at 45–80°, strongly zigzagged. Leaflets elliptic, 3.5–8 cm long, 1–4 cm wide, acute to acuminate, sparsely appressed pubescent especially on veins, sometimes glabrate above, lateral veins 7–9 pairs, very conspicuously net-veined beneath; petioles 0.7–1.7 cm long; stipules caducous, narrowly elliptic to linear, 1.5–2 cm long, 0.3–0.5(–0.8) cm wide, cuneate, acuminate. Racemes terminal, 7–20 cm long, with 5–17 flowers, scattered; peduncles 3–7 cm long; pedicels 4–6 mm long, villosulous; bracts persistent, lanceolate, 8–13 mm long, 2–4 mm wide. Flowers 1.6–1.9 cm long; calyx 7.5–8 mm long, 6–7 mm wide at the limb, lobes 2–3 mm long, shorter than tube; wings elliptic to asymmetrically oblong-elliptic; keel asymmetrically oblong-elliptic; ovary densely appressed pubescent; ovules (8–)12–16. Pods arcuate to straight, divergent, (3–)4–9 cm long, 0.4–0.6 cm wide, densely appressed pubescent. Seeds 6–12, oblong with a rostrum, 2.5–3.5 mm long, 1.5–2 mm wide. Chromosome number, $2n = 18$.

Distribution and ecology (Fig. 5). Mostly mid-elevations of the southern Appalachian Mountains and adjacent piedmont region of northernmost Georgia, eastern Tennessee, northwestern South Carolina, western North Carolina, and central Virginia, mostly 300–800 m; flowering (April–)May–June.

Representative specimens examined. U.S.A. **Alabama:** De Kalb Co., Mentone, *Loving* 1899 (US). **Georgia:** Dade Co., 1 mi. W of Durham and NE of Cloudland Canyon, 12 May 1953, *Hardin 15933* (NCU, US); Lookout Mt., 26 Apr. 1952, *Harper 4204* (NY, US). Habersham Co., near Cornelia, *Huger* 1898 (NY). Walker Co., 22.4 mi. SE of La Fayette, 24 Apr. 1961, *Turner 4691* (TEX). Whitfield Co., 4 mi. NW of Dalton, 24 Apr. 1948, *Cronquist 5055* (NY); near summit of Chattoogata Mts., 19 July 1990, *Harper 265* (NY, US). **North Carolina:** Buncombe Co., [Asheville], Biltmore, 1 May–10 June 1896, *Biltmore 1025* (F, MO, NY, PH, RM, TENN, UC, US). Caswell Co., Milton, *Fomey* 1860 (PH). Catawba Co., 3 mi. SSE of Newton, 29 Apr. 1957, *Bell 6822* (NC, NY); 1.25 mi. SW of Hickory on U.S. Hwy. 70, 3 May 1953, *Radford & Wood 6970* (NCU, US). Chatham Co., vicinity of Bush Creek, 3.9 mi. S of Orange Co. line on U.S. Hwy. 15 and 0.6 mi. E on paved road, 24 Apr. 1957, *Ahles 23825* (GH, NCU); Edward's Mt., 3 mi. E of U.S. Hwy. 501, 6.6 mi. S of Chapel Hill, 11 Apr. 1940, *Radford & Steward 77* (NCU). Durham Co., *Lynn* 1933 (ND). Forsyth Co., *Schallert* 1940 (GH); S edge of Winston-Salem, *Wherry* 1928 (NY). Gaston Co., near summit of Kings Mt., 24 Apr. 1968, *Leonard & Radford 1353* (LL, NCU, OSC, TENN, TEX); Crowders Mt., 4 June 1953, *Radford & Haesloop 7089* (ARIZ, NCU). Guilford Co., Guilford College, 30 Apr. 1958, *Terrell 3205* (NCU). Henderson Co., Flat Rock, *Memminger* 1886 (NCU). Iredell Co., 3.3 mi. W of Harmony on North Carolina Hwy. 901, 21 Apr. 1953, *Daggy 2221* (NCU); Statesville, *Hyams 4968* (F, MO, NY, POM). Lincoln Co., *Hunter s.n.* (GH, NY); near Vale, 28 Apr. 1957, *Bell 6654* (NCU). Orange Co., near Hillsboro, *Curtis s.n.* (NY). Stokes Co., 1 mi. N of Hanging Rock, 30 Apr. 1961, *Carswell 192* (NCU); above Danbury, *Hunt* 1936 (NCU). Surry Co., Pilot Mt., *Ashe* 1896

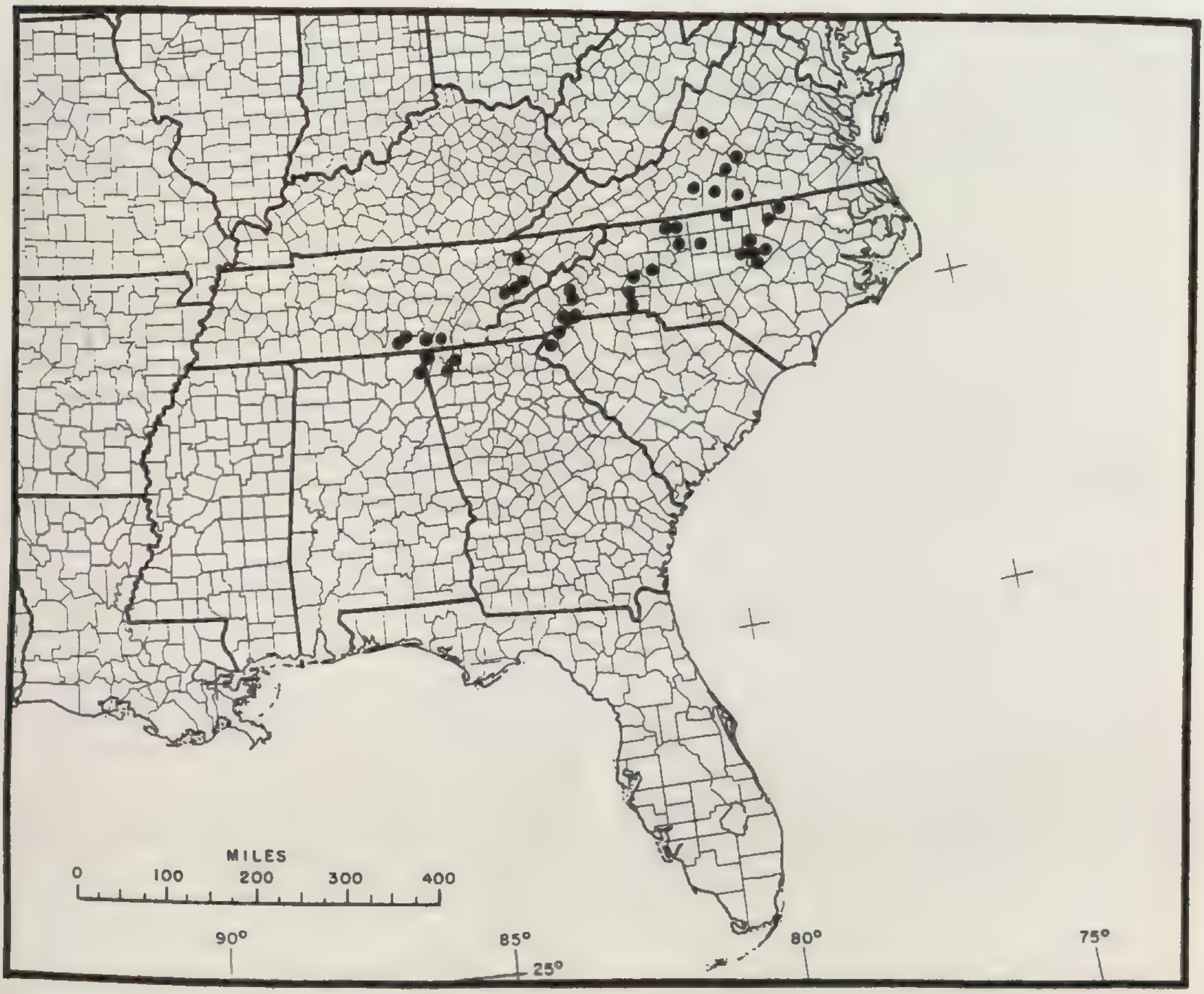

FIGURE 5. Distribution of *Thermopsis mollis*.

(NCU); Pilot Mt., 5 May 1935, *Oosting 3519* (NCU). Vance Co., Kittrell, *Browne* 1884 (NY); Kittrell's Springs, *Faxon* 1874 (GH). Wake Co., 5.5 mi. NE of Holly Springs, 28 Apr. 1954, *Radford & Beard 7984* (NCU); W of Raleigh, 1 mi. N of Tyson's Store, 30 Apr. 1951, *Fox 4580* (MO). Warren Co., Ridgeway, 20 Apr. 1938, *Godfrey 3600* (GH, NCU). **South Carolina:** Greenville Co., Paris Mt., *Huger* 1903 (NY); Paris Mt., *Huger* 1904 (NY). Oconee Co., Rich Mt., 5.5 mi. W of Walhalla, 16 Apr. 1967, *Bozeman et al. 8862* (COLO, NCU, POM, WTU); Mountain Rest, ca. 0.5 mi. W of West Village Creek on County Route 258, 30 Apr. 1989, *Hill 20511* (NY). Pickens Co., 12.5 mi. S of Rosman along U.S. Hwy. 178, 1 May 1941, *McVaugh 5649* (GH, UC). **Tennessee:** Blount Co., Chilhowee Mt., 26 Apr. 1939, *Jennison 299* (TENN); Chilhowee Mt., between Millstone Gap and Walland, *Thomas* 1965 (TENN). Franklin Co., edge of Sewanee, 3 May 1941, *Sharp & Meyer 1259* (MO, PH, TENN, UC); St. Andrews, 25 Apr. 1936, *Svenson 7592* (GH, MO, PH, UC). Grainger Co., Lea Lakes, 3 May 1934, *Hesler & Sharp 566* (TENN). Hamilton Co., Lookout Mt., *Churchill* 1906 (GH); Lookout Mt., *Churchill* 1906 (GH, MO, TENN). Marion Co., W of Whitwell, 14 May 1934, *Harger 7788* (GH, TENN). Sevier Co., Gatlinburg entrance to Great Smoky Mountains National Park, *Rogers 41851* (TENN); Chilhowee Mt., 7 May 1964, *Thomas 32794* (TENN). **Virginia:** Bedford Co., intersection of County Route 711 and County Route 811, 11 Aug. 1985, *Wright 469* (MO). Campbell Co., Sleepy Hollow Road, 23 May 1967, *Freer 5597* (GH, NCU). Charlotte Co., 4 mi. S of Charlotte, Court House township, 16 Apr. 1967, *Harvill 15436* (NCU). Halifax Co., near Halifax, *Rowlett* 1921 (US). Prince Edward Co., Hampden Sydney College, *Blair* 1981 (F, GH, MO, NY, US); Farmville, *Fattig* 1922 (US). Rockbridge Co., Balcony Falls, 1 May 1947, *Freer 1348* (GH).

The relationship of this species to *Thermopsis fraxinifolia* is discussed under *T. fraxinifolia*.

Fernald (1950) noted that at least one population of *Thermopsis mollis* from Essex Co., Massachusetts, had been introduced and naturalized in the northeastern United States, although he ignored the more widely cultivated *T. villosa*. We have examined material from Essex Co. (GH), presumably that referred to by Fernald, but it appears to be *T. villosa*.

7. **Thermopsis montana** Nutt. ex Torrey & A. Gray, Fl. N. Amer. 1: 388. 1840. TYPE: see *Thermopsis montana* var. *montana*.

Plants delicate, 2–8(–10) dm tall, glabrous to appressed pubescent or thinly villous; stems slender, erect, solitary or clustered, moderately or few-

branched, arising from a woody rootstock or rhizomes; branches ascending at 20–45°, weakly to moderately zigzagged. Leaflets narrowly elliptic or obovate, 3.5–8 cm long, 0.7–3(–5) cm wide, acute or obtuse, sometimes short mucronate or emarginate, sparsely appressed pubescent to glabrous, lateral veins 6–11 pairs, conspicuously net-veined beneath or not; petioles 1–4 cm long; stipules persistent, widely ovate or elliptic, 1.7–4.5 cm long, 0.7–2.5 cm wide, oblique to cuneate, acuminate or acute. Racemes 4–25 cm long, with 6–25 flowers, in whorls of 2–3 or scattered; peduncles 2–8 cm long; pedicels 3.5–5 mm long, villosulous; bracts semipersistent, narrowly elliptic to widely ovate, 6–10 mm long, 2.5–6 mm wide. Flowers 1.6–2.2 cm long; calyx 9–11 mm long, 5–8 mm wide at the limb, lobes 3–5 mm long, shorter than tube; wing and keel petals asymmetrically oblong-elliptic; ovary velutinous or densely appressed pubescent; ovules 10–16. Pods straight, erect, 4.5–6.5 cm long, 0.4–0.6 cm wide, villosulous or appressed pubescent. Seeds 6–16, brown-black, oblong with a rostrum, 3.5–5 mm long, 2.5–3 mm wide.

We recognize two intergrading varieties under this taxon, as follows:

KEY TO VARIETIES OF *THERMOPSIS MONTANA*

1a. Plants less than 7 dm tall, pubescent; stems often solitary and few-branched, often arising from rhizomes; leaflets not conspicuously net-veined beneath; bracts elliptic to widely ovate ——— 7a. *Thermopsis montana* var. *montana*

1b. Plants up to 10 dm tall, glabrate; stems clustered and moderately branched, arising from a woody rootstock; leaflets conspicuously net-veined beneath; bracts narrowly elliptic ——— 7b. *Thermopsis montana* var. *ovata*

7a. Thermopsis montana var. **montana.**

Thermopsis fabacea var. *montana* (Nutt. ex Torrey & A. Gray) A. Gray, Proc. Acad. Nat. Sci. Philadelphia 1863: 60. 1864. *Thermopsis rhombifolia* var. *montana* (Nutt. ex Torrey & A. Gray) Isely, Brittonia 30: 470. 1978. TYPE: U.S.A. Wyoming: "Rocky Mountains" [Sweetwater Co.?], *Nuttall* 1834 (holotype, BM not seen; photo of holotype, POM, UK; isotype, PH; photo of isotype, POM).

Thermopsis angustata E. Greene, Pl. Baker. 3: 34. 1901. TYPE: U.S.A. Nevada: Elko Co., Star Valley, "foothills of the Ruby Mountains," *E. L. Greene* 1896 (holotype, ND).

Thermopsis stricta E. Greene, Pl. Baker. 3: 34. 1901. TYPE: U.S.A. Colorado: Gunnison Co., Gunnison, 24 July 1901, 2330 m, *C. F. Baker 604* (lectotype, selected here, ND; isolectotypes, GH [2 sheets], NY RM [2 sheets], UC, US [2 sheets]).

According to the known distribution of *Thermopsis montana*, Nuttall would most likely have first encountered the species in Sweetwater Co., Wyoming, at about the time indicated. It is also possible that it was first collected in southeastern Idaho in early July (cf. Graustein, 1967).

Plants 2–7 dm tall, appressed pubescent to thinly villous; stems stiffly erect, solitary or clustered, few-branched, arising from a woody rootstock or rhizomes; branches moderately zigzagged. Leaflets elliptic to narrowly elliptic or obovate, 3.5–8 cm long, 0.7–2.5 cm wide, appressed pubescent, not conspicuously net-veined beneath; petioles 1–2.5 cm long. Racemes 4–18 cm long; bracts elliptic to widely ovate. Flowers 1.6–2 cm long. Pods villosulous. Chromosome number, $2n = 18$.

Distribution and ecology (Fig. 6). Widely distributed in the intermountain region of the United States, from southwestern Montana southward to Arizona and New Mexico and northwestward to southern Idaho and adjacent Wyoming, middle to high elevations, 2000–3200 m; flowering May–June.

Representative specimens examined. U.S.A. **Arizona:** Apache Co., 1 mi. N of Alpine, 27 June 1944, *Pultz & Phillips 1030* (ARIZ, NY, UC). Cochise Co., Barefoot Park, *Blumer* 1907 (ARIZ, F, GH, MO, NY, RM, US). Coconino Co., Flagstaff, 21 Apr. 1925, *Nelson 10200* (GH, MO, NY, PH, POM, RM, UC, WS). Gila Co., Sierra Ancha, Aztec Peak, 1 May 1931, *Harrison 7857* (ARIZ, US). Graham Co., Graham Mts., Pine Crest, 26 May 1935, *Maguire 12013* (NY, WS, WTU). Greenlee Co., near Rose Peak, 43 mi. N of Clifton, 7 June 1935, *Maguire 11886* (ARIZ, GH, NY, UC). Navajo Co., head of Little Colorado, 10 July 1912, *Goodding 1147* (ARIZ, NY, RM, US). Yavapai Co., S of Prescott, 2 June 1944, *Clark 11770* (GH, US). **Colorado:** Archuleta Co., Piedra, near Piedra River, 18 June 1924, *Schmoll 1122* (RM). Chaffee Co., Poncha Springs, at intersection of railroad and highway along creek bed, 27 May 1968, *Turner 5777* (TEX). Clear Creek Co., Brookvale, Bear Creek, *Churchill* 1918 (GH, MO). Conejos Co., SW of La Jara Reservoir, 19 Aug. 1986, *O'Kane & Anderson 2618* (RM). Costilla Co., 61 mi. E of Montevista, La Veta Pass, 30 May 1934, *Frederick & Stone 608* (NY). Custer Co., W of Westcliffe, trail to Lakes of the Clouds, 29 July 1950, *Weber 5894* (COLO). Delta Co., Mule Park, 12 July 1962, *Gierisch 2552* (RM). Dolores Co., Lone Cone, along water courses, *Brewster s.n.* (COLO). Eagle Co., McCoy, edge of meadow, 30 July 1898, *Shear 5310* (RM). Garfield Co., *Glenwood* 1910 (GH). Gunnison Co., Sapinero, 19 June 1901, *Baker 173* (MO, RM, ND, NY, POM, UC). La Plata Co., 10 mi. W of Durango, 20 June 1965, *Strother 389* (TEX). Las Animas Co., Wilkins Creek, ca. 0.25 mi. NW of Stonewall Gap, 15 Aug. 1987, *Neely 4635* (RM). Mesa Co., Uncompahgre Plateau, head of Escalante Canyon, 19 July 1982, *Siplivinsky & Beck 4251* (COLO, RM). Mineral Co., Wolf Creek Pass, U.S. Hwy. 160, 3 mi. below summit on E side, 27 Aug. 1964, *Turner 5099* (TEX). Montezuma Co., along Dolores Riv-

er, Escalante Sector, *Bye et al.* 1978 (COLO). Montrose Co., 30 mi. SW of Montrose, 28 Aug. 1937, *Rollins 1978* (CAS, GH, MO, ND, NY, RM, US). Ouray Co., *Clements* 1907 (NY). Rio Blanco Co., 2 mi. E of Meeker, 18 Aug. 1935, *Maguire & Piranian 12844* (MO). Park Co., Jefferson South Park, 9 Sep. 1942, *Ewan 14706* (COLO). Rio Grande Co., along South Fork of Rio Grande River, 27 Aug. 1964, *Turner 5095* (TEX). Saguache Co., Marshall Pass, 21 July 1960, *Barrell 127-60* (US). **Idaho:** Bannock Co., E of Lava Hot Springs, *Everson* 1946 (NY). Bear Lake Co., 1.3 mi. N of St. Charles, 25 June 1967, *Faircloth 4548* (NCU). Bingham Co., Ft. Hall, *Everson* 1942 (TEX). Caribou Co., 8 Mile Canyon, 12 mi. S of Soda Springs, 28 June 1960, *Cottam et al. 16280* (UT). Cassia Co., 20 mi. S of Oakley, along Goose Creek, 2 July 1950, *J. H. & C. B. Christ 19580* (WS). Clark Co., Kaufman, near Birch Creek, 19 July 1934, *Christ 5818* (NY). Elmore Co., Moore's Creek, Boise River tributary, *Grandjean 155* (RM). Franklin Co., 11 mi. NE of Preston, 5 mi. up Millcreek Canyon, 14 May 1966, *G. & G. Davidse 391* (UC, US, WTU). Lemhi Co., 20 mi. E of Gilmore, along Birch Creek, 25 June 1947, *Hitchcock 15766* (CAS, COLO, MO, NY, PH, POM, RM, UC, WS, WTU). Oneida Co., divide between Marsh and Malad Valleys, *Coulter s.n.* (PH). Owyhee Co., ca. 39 mi. S of Bruneau, 30 May 1968, *Turner 5798* (NY, RM, TEX). Twin Falls Co., Twin Falls, 26 May 1912, *Bennett 88* (RM). **Montana:** Beaverhead Co., Armstead, 20 June 1920, *E. B. & L. B. Payson 1734* (CAS, GH, MO, RM). Broadwater Co., 4 mi. SE of Townsend, 10 June 1960, *Schmautz JES-345* (CAS, RM, WS). Deerlodge Co., Fishtrap, ca. 25 mi. S of Anaconda, 20 June 1944, *Hitchcock & Muhlick 9173* (CAS, GH, MO, NY, RM, UC, WS, WTU). Gallatin Co., Belgrade, low ground, 2 June 1906, *Blankenship 681* (F, MO, POM, RM, UC, US). Jefferson Co., Boulder, 24 Apr. 1939, *Rose 709* (RM). Madison Co., Virginia City, *Swingle* 1933 (RM, WTU). Powell Co., vicinity of Deer Lodge, *Fitch s.n.* (RM). Silver Bow Co., Lower Moose Creek, ca. 1 mi. N of Moose Creek Parking Area, 28 June 1979, *Lowry 2270* (RM). **Nevada:** Elko Co., 3 mi. N of Ruby Valley on E side of Ruby Mts., 29 May 1968, *Turner 5795* (TEX). Eureka Co., Eureka, 2 July 1904, *Kennedy 838* (ARIZ, MO, RM, UC). Humboldt Co., Santa Rosa Range, NE of Winnemucca, 29 June 1967, *Gentry & Davidse 1674* (ARIZ, COLO, GH, MO, NY, OSC, POM, UC, WTU). Lander Co., Reese River Valley, U.S. Hwy. 50, along edge of Reese River, 13 June 1964, *Spellenberg 370* (F, NY). Lincoln Co., Geyser Ranch, 28 May 1945, *Ripley & Barneby 6436* (NY). Nye Co., Darrough Hot Springs, Smoky Valley, 11 May 1939, *Train 2743* (MO, NY, POM, TEX, UC, WTU). White Pine Co., canyon E of Mt. Grafton, 11 Aug. 1969, *Holmgren & Bethers 3861* (NY, POM, US, WTU). **New Mexico:** Bernalillo Co., 8.5 mi. from San Antonito, 0.7 mi. N of Capulin Spring, 21 May 1967, *Turner 5649* (CAS, NY, TEX). Catron Co., Mogollon Mt., near West Fork of the Gila River, 23 Aug. 1903, *Metcalfe 593* (MO, ND, NY, RM, US). Colfax Co., 1 mi. NW of Ute Gulch Camp, 17 June 1968, *Hartman 1973* (RM, TEX). Grant Co., Pinos Altos, 2.6 mi. by road to Signal Peak E of New Mexico Hwy. 15, 25 May 1985, *Worthington 13180* (NY, RM). Lincoln Co., Sierra Blanca, valley of Carrizo Creek, 11 June 1932, *Wilkins 2402* (PH, US); McKinley Co., Long Canyon, 6 mi. S of Crownpoint, *Jump 1974* (ARIZ). Mora Co., 1 mi. E of La Cueva, *Stiteler* 1949 (PH). Otero Co., near summit of pass between Hollywood and Mescalero, 26 May 1934, *Ferguson & Ottley 5223* (UC). Rio Arriba Co., Ortega Mts., ca. 2 mi. W of Hopewell Lake, 17 Aug. 1984, *Hill 15167* (NY). San Miguel Co., 8 mi. E of Glorietta, along the Pecos River, 9 June 1897, *A. A. & E. G. Heller 3681* (MO, NY, US). Sandoval Co., 24 mi. N of Jemez Pueblo, 6 June 1974, *Atwood 6249* (NY). Santa Fe Co., near Santa Fe Recreation Area, just off New Mexico Route 475, 16 June 1964, *Perdue 6047* (US). Taos Co., Penasco, Santa Barbara Canyon, 7 July 1936, *Marcelline 1989* (F). **Oregon:** Crook Co., 5 mi. W of Prineville, 15 June 1928, *Pech 15964* (OSC, PH). Grant Co., 3 mi. E of Canyon City, 5 June 1953, *Cronquist 7087* (GH, NY, WS, WTU). Harney Co., 23 mi. S of Frenchglen, 16 May 1959, *Cronquist 8245* (GH, NCU, NY, POM, RM, TEX, UC, WS, WTU) [approaches variety *ovata*]. Malheur Co., 3 mi. W of McDermitt, 25 June 1934, *Peck 21734* (OSC, UC). **Utah:** Beaver Co., Wah Wah Mts., Birch Creek, 4 May 1937, *Cottam 7109* (UT). Box Elder Co., Brigham City, 9 May 1910, *Smith 2120* (GH, NY). Cache Co., 0.25 mi. E of Wellsville, 30 May 1940, *Maguire 18600* (NY, WTU). Daggett Co., vicinity of Flaming Gorge, 29 May 1932, *Williams 432* (GH, MO, NY, RM). Duchesne Co., 5 mi. N of Duchesne, 6 June 1979, *Neese & Welsh 7503* (NY). Garfield Co., 7 mi. SE of Boulder, Deer Creek, 4 May 1977, *Foster 3661* (NY, UT). Grand Co., 2 mi. N of Warner Ranger Station, La Sal Mts., 8 July 1933, *Maguire 313* (UC, WTU). Iron Co., ca. 15 mi. E of Cedar City, just W of the entrance to Dixie National Forest, 13 June 1969, *Meyer 356* (UT). Millard Co., Simonsen's Ranch, along irrigation stream, 16 June 1933, *Maguire & Becraft 3932* (GH, UC). Morgan Co., flat area below dam by old gauging station, 17 May 1987, *Peterson 14* (NY, UT). Piute Co., 5 mi. E of Kingston on Utah Hwy. 62, 3 May 1977, *Foster 3613* (NY, RM). Rich Co., W shore of Bear Lake, 0.7 mi. E of Pickleville, 5 July 1985, *Thorne 3938* (GH, MO). Salt Lake Co., vicinity of Salt Lake City, *Clements* 1908 (F, GH). Sevier Co., 3 mi. S of Sevier, along stream, 8 May 1937, *Hitchcock 2947* (GH, RM, UC, WS, WTU). San Juan Co., ca. 80 mi. S of Moab, NW flank of Abajo Mts., 12 June 1961, *Cronquist & Holmgren 9259* (GH, NY, NCU, POM, TEX, WS, WTU). Summit Co., Goodman Ranch near Bear River, 30 June 1926, *E. B. & L. B. Payson 4833* (MO, PH, POM, RM, UC, US); Uintah Co., E of Hayden, along Uintah River, 2 June 1933, *Graham 8044* (F, GH, NY, US). Utah Co., near top of Price Canyon, *Malburtt* 1959 (UT). Wasatch Co., 6 mi. N of Heber City, along highway, 28 May 1968, *Turner 5794A & 5794B* (TEX). Washington Co., 5 mi. SW of Enterprise at Aspen Park Spring, 10 June 1903, *Atwood 9366* (NY, RM). Wayne Co., Fruita, 18 May 1956, *Vickery 587* (ARIZ, GH, POM, UT, WTU). Weber Co., Huntsville, 26 May 1940, *Brizzee 7794* (UT). **Wyoming:** Carbon Co., Baggs, 4 July 1926, *Nelson 10720* (GH, MO, RM, UC). Park Co., *McCosh* 1878 (NY). Sweetwater Co., Uinta Mts., Henrys Fork, river bottoms, 26 June 1902, *Goodding 1192* (CAS, F, GH, MO, NY, POM, RM, UC). Uinta Co., 1 mi. S of Lonetree, 27 July 1939, *Rollins & Munoz 2903* (CAS, GH, US).

Thermopsis montana var. *montana* is widespread and highly variable but can usually be distinguished from variety *ovata* by its smaller habit, narrower leaflets and bracts, and greater tendency to spread by rhizomes. In southwestern Oregon the

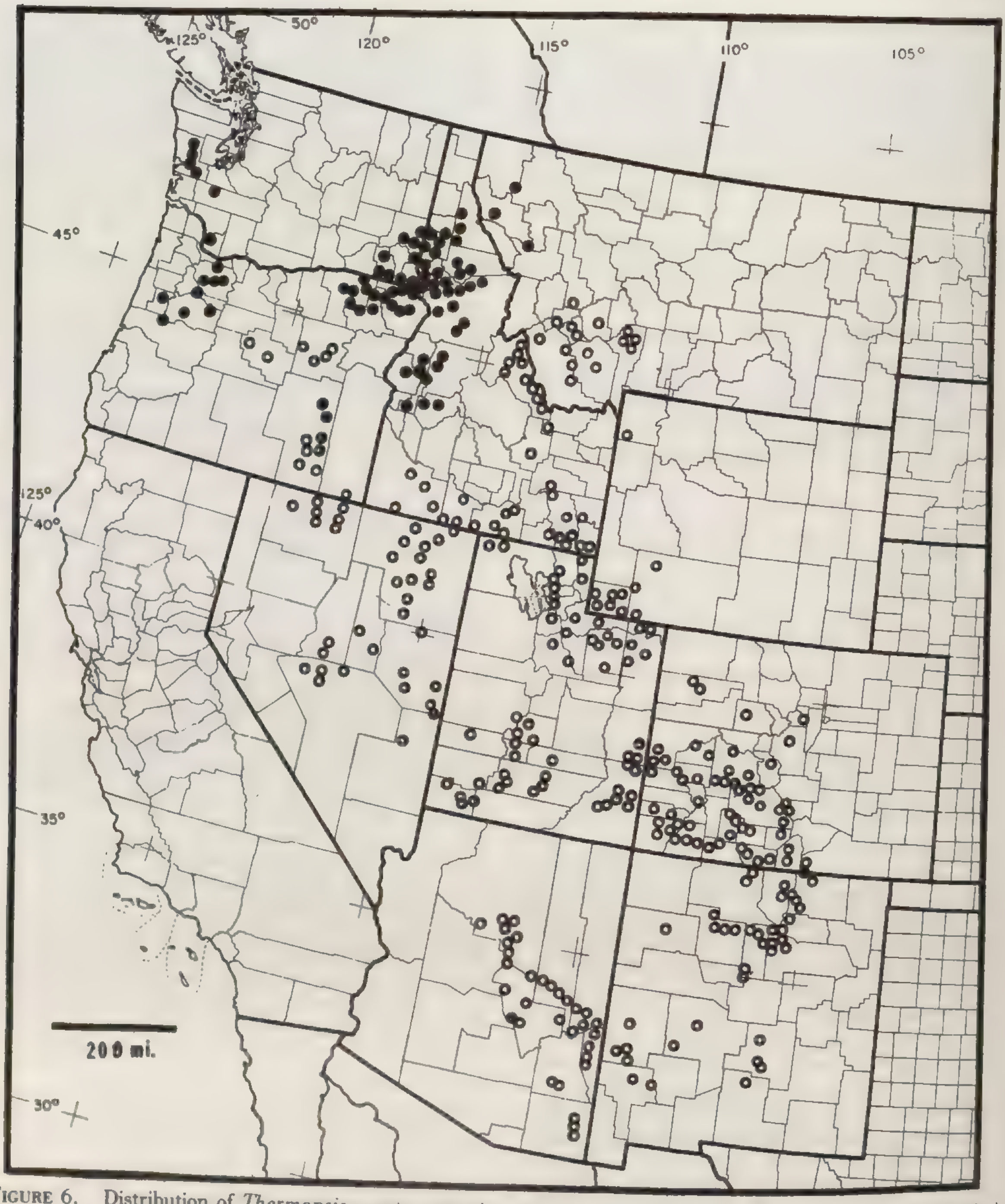

FIGURE 6. Distribution of *Thermopsis montana*: variety *montana* (open circles); variety *ovata* (closed circles).

taxa appear to intergrade. Isely (1981) recognized a "Lemhi race" (Lemhi County, Idaho) within the taxon we call *T. montana* var. *montana*. Though with somewhat broader leaflets, most of those specimens are fairly typical of *T. montana* var. *montana*.

In Arizona and most of New Mexico (from below San Juan and Rio Arriba counties) there also occurs a series of populations that are composed of rather broad-branching plants with leaves more or less like *Thermopsis montana* var. *ovata*. Unlike Isely (1981), we do not find such plants in Colorado.

The strictly erect pods distinguish *Thermopsis montana* from *T. gracilis* and from the superficially similar *T. divaricarpa*. Isely (1981) treated *T. montana* and *T. divaricarpa* as varieties of a widespread, extremely variable *T. rhombifolia*. We have found that *T. rhombifolia*, *T. divaricarpa*, and *T. montana* are clearly distinct throughout most of their ranges and do not appear to intergrade as do *T. montana* var. *montana* and *T. montana* var. *ovata*. Intermediate populations and possible hybrids are discussed under *Thermopsis divaricarpa*.

7b. Thermopsis montana var. **ovata** (Robinson ex Piper) St. John, Torreya 41: 112. 1941. *Thermopsis montana* subsp. *ovata* Robinson ex Piper, Contr. U.S. Natl. Herb. 23: 49. 1906. *Thermopsis ovata* (Robinson ex Piper) Rydberg, Bull. Torrey Bot. Club 40: 43. 1913. *Thermopsis rhombifolia* var. *ovata* (Robinson ex Piper) Isely, Brittonia 30: 470. 1978. TYPE: U.S.A. Idaho: Latah Co., "Cedar Mountain," 4 July 1893, *C. V. Piper 1489* (lectotype, selected here, WS; isolectotypes, GH, US, WS).

Thermopsis xylorhiza Nelson, (*xylorrhiza auct.*), Bot. Gaz. 52: 265. 1911. TYPE: U.S.A. Idaho: Canyon Co., Falk's Store, 667 m, 24 May 1910, *J. F. Macbride 99* (holotype, RM; isotypes, GH, MO, NY, RM, UC, WS).

Thermopsis macrophylla var. *hitchcockii* Isely, Brittonia 30: 469. 1978. TYPE: U.S.A. Washington: Grays Harbor Co., roadside near Humptulips, 10 July 1931, *J. W. Thompson 7342* (holotype, WTU; isotypes, GH, OSC, PH, POM, UC).

Piper's collection number *1489* was apparently a mixture of plants collected on 16 June 1893, 4 July 1893 (in fruit), and 21 June 1894 (in flower). We have selected the fruiting specimen as the lectotype. It is assumed that all of the collections came from the same site, although this is not certain because some of the labels (21 June 1894, NY) give the locality as "along streams in woods." The published type locality is given by Peck as "Cedar Mountain"; this locality was not on any of the labels numbered *1489* that we examined.

Plants 5–8(–10) dm tall, glabrate to sparsely appressed pubescent; stems erect, clustered, moderately branched, arising from a woody rootstock; branches weakly to moderately zigzagged. Leaflets broadly to narrowly elliptic or obovate, 4.5–6(–8) cm long, 1.5–3(–5) cm wide, sparsely appressed pubescent below, glabrous above, conspicuously net-veined beneath; petioles 3.2–4 cm long. Racemes 12–25 cm long; bracts narrowly elliptic. Flowers 1.9–2.2 cm long. Pods appressed pubescent.

Distribution and ecology (Fig. 6). Columbia and Snake River drainages of northern Idaho and adjacent states of Wyoming, Washington, and Oregon, with isolated populations along the Pacific coast of Washington and northwestern Oregon, 300–2000 m in the upper river drainages but mostly at lower elevations (10–200 m) about the mouth of the Columbia River and its immediate tributaries; flowering May–June.

Representative specimens examined. U.S.A. **Idaho:** Ada Co., 13 mi. E of Boise, Moore's Creek Canyon, 14 June 1947, *J. H. & C. B. Christ 16858* (NY). Adams Co., *Davis* 1939 (WS); Hornet, 13 May 1915, *Mangun 139* (RM). Boise Co., 15 mi. W of Lowman, above Payette River, on road between Banks and Lowman, 31 May 1944, *Hitchcock & Muhlick 8563* (NY, WS, WTU). Butte Co., *Christ 3386* (NY). Canyon Co., Falk's Store, 10 May 1911, *Macbride 800* (F, GH, MO, NY, POM, RM, UC, US, WS, WTU). Clearwater Co., Clearwater Forest, Lolo Creek, 16 Oct. 1934, *Christ 6322* (NY); 5 mi. W of Orofino, S side of the Clearwater River, 5 May 1951, *Roeder 241* (WS). Idaho Co., 0.5 mi. from Pilot Rock, *Elwood 51* (CAS, NY, POM, UC, WS, WTU); 7 mi. SE of Elk City, 14 June 1950, *Jones 14* (CAS, GH, POM, WS, WTU); 2 mi. S of Grangeville, 29 May 1944, *Hitchcock & Muhlick 8455* (CAS, NY, RM, UC, WS, WTU). Latah Co., wooded hills just W of Troy, 24 May 1964, *Hitchcock 23465* (CAS, NY, UC, WS, WTU). Lewis Co., Mission Creek, 30 May 1924, *John et al. 6334* (UC, WS, WTU). Nez Perce Co., Aug. 1898, *Brown 6* (CAS, MO, ND, NY, PH, UC, US); 3 mi. below Lowell, 30 May 1936, *Constance & Rollins 1621* (F, GH, NCU, MO, NY, RM, UC, PH, WS, WTU); near Lewiston, 7 May 1896, *A. A. & E. G. Heller 3035* (CAS, F, MO, ND, NY, PH, UC, WTU); valley of Hatwai Creek, 28 Apr. 1892, *Sandberg et al. 68* (ARIZ, F, GH, MO, NY, POM, US). Shoshone Co., 8 mi. N of Calder, along St. Joe River, 19 May 1940, *Christ 10969* (NY); Clearwater Camp on the Little North Fork of the Clearwater River, 4 Aug. 1941, *Wilson 467* (WS). Valley Co., 5 mi. W of McCall, 24 June 1946, *Hitchcock & Muhlick 13937* (CAS, MO, NY, POM, RM, UC, WS); 9 mi. E of McCall, 11 July 1953, *Holmgren & Tillett 9542* (GH, NY, OSC, UC, WTU). Washington Co., S of Council, wet meadows along highway, 11 May 1939, *Cronquist 1151* (NY). **Montana:** Sanders Co., Dixon, 31 May 1937, *Brome 28* (MO, PH, RM, WTU); 2 mi. W of Dixon, Wolf Point, 13 May 1936, *Hitchcock 2877* (MO, ND, OSC, RM, WS, WTU). **Oregon:** Clackamas Co., Eagle Creek, high hills, 24 May 1884, *Henderson 179* (OSC, PH, WS); near base of Table Rock, *Leach* 1927 (WTU). Linn Co., Monument Peak, *Gilkey* 1947 (OSC, POM). Marion Co., Silverton, Spring 1871, *Hall 83* (F, POM); 6 mi. E of Brownsville, Cascade Mts., 18 June 1918, *Lawrence 1751* (OSC, US); Silver Creek Falls, 19 June 1918, *Nelson 2257* (GH). Polk Co., 2 mi. W of Grand Ronde, *Brehm* 1967 (TEX). Umatilla Co., 1 mi. SE of Meacham, 23 June 1946, *Hitchcock & Muhlick 13841* (CAS, GH, MO, NY, OSC, UC, WS, WTU); between Pendleton and LaGrande, near summit of Blue Mts., 14 June 1928, *Thompson 4723* (CAS, GH, MO, US, WTU). Union Co., Kamela, 1 June 1910, *Heller 10145* (CAS, GH, PH, UC); 2 mi. S of Elgin, 20 May 1975, *Watkins & Dunn 95* (MO, NY). Wallowa Co., along summit of road between Elgin and Langdon Lake, 28 July 1950, *Kruckeberg 2487* (CAS, COLO, GH, NY, RM, UC); Walupi Canyon, 18 Aug. 1897, *Sheldon 8724* (NY, US). **Washington:** Asotin Co., Snake River, just below the mouth of the Grande Ronde, 17 Apr. 1949, *Cronquist 5701* (GH, NY, POM, UC, US, WS, WTU); SW of Anatone, along Grande Ronde River, just above Rattlesnake Creek, 22 Apr. 1949, *Cronquist 5709* (GH, NY, POM, UC, US, WTU). Columbia Co., Dayton, between hospital and Touchet River, 3 May 1983, *Baird 51* (NY); Blue Mts., 4 mi. N of Table Rock, 20 July 1935, *Constance et al. 1278* (MO, WS). Grays Harbor

Co., N of Aberdeen and Hoquiam along U.S. Hwy. 101, 31 May 1987, *Boufford & E. W. Wood 23757* (A, CAS, MO, NCU, NY); ca. 20 mi. N of Hoquiam, 24 June, *Hitchcock 19872* (COLO, OSC, POM, UC, WTU); between New London and Humptulips, 28 June 1933, *Jones 3937* (CAS, POM, RM, UC, WTU); open burns near Humptulips, 30 May 1940, *Thompson 14606* (CAS, GH, MO, NY, PH, POM, RM, UC, US). Lewis Co., Chenalis, Oxford Prairie, 12 June 1897, *Lamb 1197* (CAS, F, MO, NY, PH, UC, WS). Walla Walla Co., 2 mi. S of Walla Walla, 24 May 1944, *Hitchcock & Muhlick 8274* (CAS, NY, RM, UC, WS, WTU); 1 mi. NE of Walla Walla, flats near Mill Creek, 2 May 1936, *Moore 23* (UC, WS). Whitman Co., 1 mi. N of Colfax, 18 May 1935, *Hitchcock & Samuel 2594* (OSC, RM); Kamiack, 15 June 1893, *Moore 1489* (US, WTU); Dusty, 3 mi. W of Colfax, 14 May 1922, *Parker 355* (NY, OSC, POM, WS).

This variety differs from *Thermopsis montana* var. *montana* in its relatively robust habit, moderately branched stems, and broader leaflets and bracts.

Plants similar to *Thermopsis montana* var. *ovata* also occur as populational variants in Arizona, most of New Mexico, parts of southern Utah, and occasionally in Colorado, as discussed under *T. montana* var. *montana*. Our treatment is like that of Isely (1981), who positioned variety *ovata* within his broad *T. rhombifolia*, except that we would include his *T. macrophylla* var. *hitchcockii* within *T. montana* var. *ovata*. We do not believe that the Pacific coast plants (= *T. macrophylla* var. *hitchcockii*, sensu Isely) differ appreciably from plants of the interior montane regions that Isely places within *T. rhombifolia*. The disjunct distribution of the Pacific coastal populations is thought to represent founder populations, perhaps dispersed by periodic flooding events and subsequent establishment of propagules from populations along the upper Columbia and Snake River drainages. One may assume that these northern Pacific coast populations are more closely related to the southern populations of *T. californica*, as suggested by Isely's treatment. Although both taxa have upright pods, the distribution of *T. californica* is interrupted in Oregon by the quite distinctive *T. gracilis*, which has divergent pods. All of the specimens of *T. montana* var. *ovata* that we have examined (including the Pacific coastal populations) have strictly erect pods, yet have other characters of the Rocky Mountain species, namely *T. montana* var. *montana*. If one accepts the taxonomic concepts espoused by Isely (1981) in which *T. divaricarpa* and *T. montana* are reduced to varietal entities of a widespread, highly variable *T. rhombifolia*, one is compelled by morphological considerations to include both *T. gracilis* and *T. californica* also as part of the *T. rhombifolia* complex, the morphological boundaries between *T. montana* var. *ovata* and *T. californica* being at least as weak as those between *T. rhombifolia* and *T. divaricarpa* or *T. montana*.

8. Thermopsis rhombifolia (Nutt. ex Pursh) Richardson, Bot. App. 737. 1823. *Thermia rhombifolia* (Pursh) Nutt., Gen. N. Amer. Pl. 1: 282. 1818. *Scolobus rhombifolius* (Nutt. ex Pursh) Raf., Amer. Monthly Mag. Crit. Rev. 4: 193. 1819. *Drepilia rhombifolia* (Nutt. ex Pursh) Raf., N. Fl. 2: 53. 1837. TYPE: U.S.A. North Dakota: Mercer Co., near Fort Mandon, *Bradbury* 1810 (lectotype, selected here, PH, A. B. Lambert herbarium).

Thermopsis arenosa Nelson, Bot. Gaz. 25: 276. 1898. *Thermopsis rhombifolia* var. *arenosa* (Nelson) Larisey, Ann. Missouri Bot. Gard. 27: 251. 1940. TYPE: U.S.A. Wyoming: Albany Co., Laramie Hills, 16 June 1897, *A. Nelson 3182* (holotype, RM; isotypes, ND, RM, [2 sheets] UC, US).

Thermopsis annulocarpa Nelson, Bull. Torrey Bot. Club 26: 239. 1899. *Thermopsis rhombifolia* var. *annulocarpa* (Nelson) L. Williams, Ann. Missouri Bot. Gard. 23: 450. 1936. TYPE: U.S.A. Wyoming: Carbon Co., Ferris Mountains, vicinity of Fort Steele, "among the rocks on the naked slopes near their summits," 25 July 1898, *Elias Nelson 4971* (holotype, RM; isotype, NY).

Larisey (1940) designated a Nuttall collection (PH) as the type of *Thermopsis rhombifolia*; however, Pursh cited only a *Bradbury* collection, listing *Cytisus rhombifolius* Nutt. as a nomen nudum from Fraser's *Catalogue* without citing a Nuttall collection.

Plants dwarf but robust, 1.2–3 dm tall, glabrate to appressed pubescent; stems slender, erect, or ascending, solitary or clustered, few-branched, arising from a woody rootstock or rhizomes; branches ascending at 25–50°, weakly zigzagged. Leaflets elliptic to obovate or narrowly elliptic, 1.7–3.3 cm long, 0.6–2 cm wide, acute to obtuse, sometimes short mucronate, appressed pubescent to sparsely tomentose or glabrate below, glabrous above, lateral veins 5–7 pairs, conspicuously net-veined beneath; petioles 0.8–2.2 cm long; stipules persistent, ovate to very widely ovate or elliptic to widely elliptic, 1–2.6 cm long, 0.5–1.5(–2.2) cm wide, cuneate to oblique, acute to obtuse and short mucronate. Racemes 4–12 cm long, with 5–15 flowers, in whorls of 2–3 or scattered; peduncles 1–4 cm long; pedicels 3–7 mm long, glabrate to densely appressed pubescent; bracts deciduous, el-

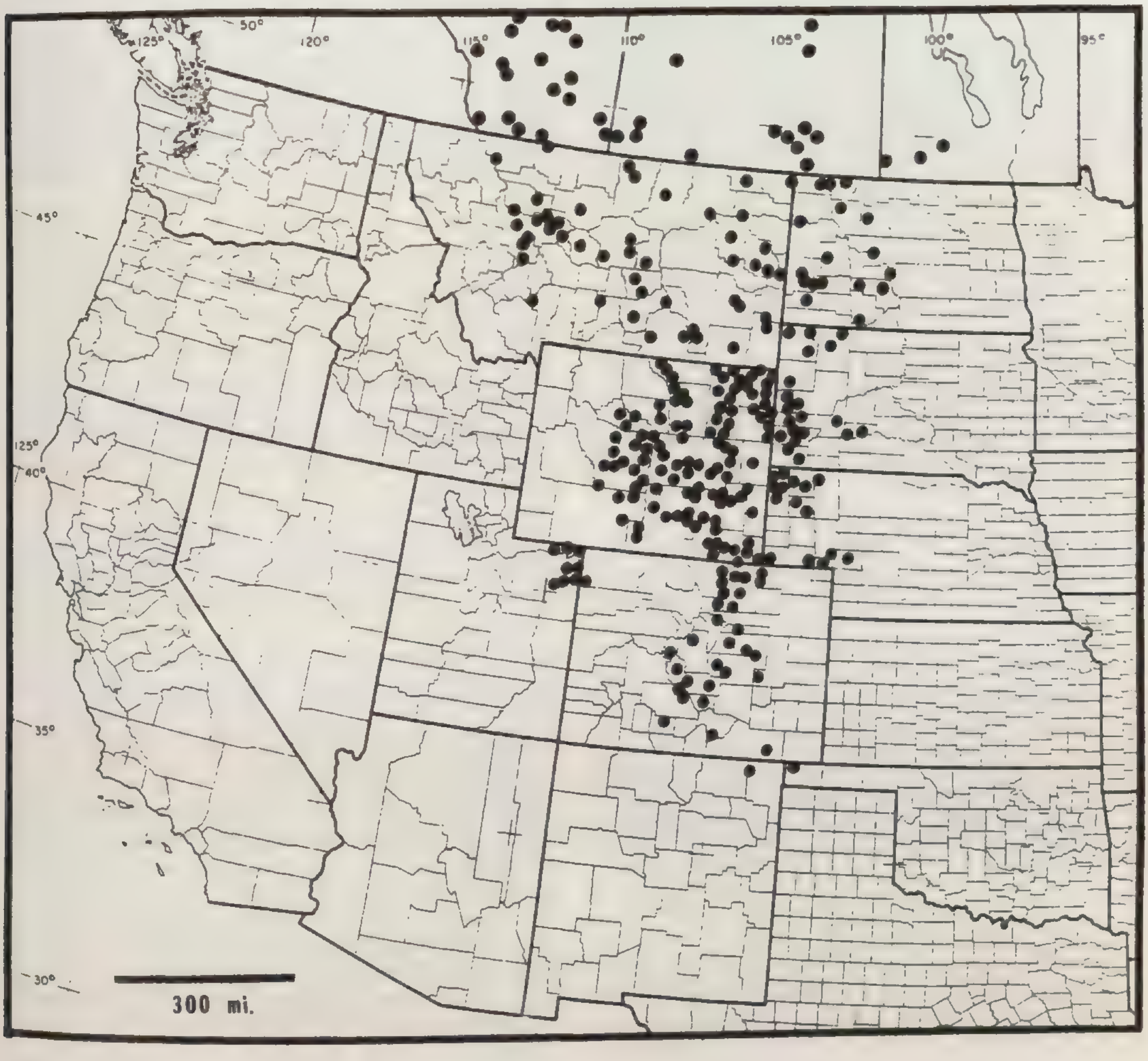

FIGURE 7. Distribution of *Thermopsis rhombifolia.*

liptic to obovate, 5–9 mm long, 3–5 mm wide. Flowers 1.9–2.1 cm long; calyx (6–)8–10(–12) mm long, 4.5–6 mm wide at the limb, lobes (3–)4–5 mm long, as long as or shorter than tube; wings asymmetrically oblong–very widely ovate; keel asymmetrically oblong–widely elliptic; ovary glabrate to appressed puberulent; ovules 12–14. Pods arcuate to annular, divergent, 3–7 cm long, 0.4–0.7 cm wide, glabrate to sparsely tomentose. Seeds 2–10, brown, elliptic with a rostrum, 3.5–4 mm long, 2.5 mm wide. Chromosome numbers $2n = 18$.

Distribution and ecology (Fig. 7). Central Great Plains of Canada and the United States from central Alberta and Saskatchewan to northeasternmost New Mexico, largely confined to relatively xeric grasslands in deep alluvial soils but extending into the lower canyons of the front range of the Rocky Mountains, 1000–2000 m, to 3000 m along roadsides; flowering May–June.

Representative specimens examined. CANADA. **Alberta:** ca. 26 km NE of Edmonton, 1 km SW of Fort Saskatchewan, 20 June 1959, *Shetler & Stone 3034* (US); 20 km W of Cochrane, 1 July 1979, *Watton 24* (COLO, MO, NY, OSC, PH). **Manitoba:** on side of Manitoba Hwy. 1 in the sand hills, 9 June 1950, *Dore 10658* (GH, NY). **Saskatchewan:** Cypress Hills Provencial Park, 1 July 1947, *Breitung 4200* (MO, RM). U.S.A. **Colorado:** Arapahoe Co., near Denver, 13 May 1917, *Clokey 2793* (ARIZ, F, GH, RM, TEX, UC, US). Boulder Co., 10 mi. NE of Boulder, White Rocks, on Gunbarrel Hill, 18 May 1967, *Turner 5634* (RM, TEX). Chaffee Co., 5 mi. SW of Buena Vista, 13 June 1967, *Johnson 80* (MONTU, NCU, TEX). Douglas Co., 2 mi. W of Franktown, 27 June 1937, *Beetle 1477* (CAS, NY, WTU). Elbert Co., 2 mi. N of Simla, 23 June 1937, *Ownbey 1296* (COLO, GH, MO, MONTU, NY, RM, UC, WS). El Paso Co., near Ramah, 25 May 1947, *Moldenke 19401* (PH, RM). Jefferson Co., E of Golden, 8 May 1941, *Ehlers 8064* (COLO, TEX). Lake Co., Tennessee Fork, 16 June 1933, *Applegate 8524* (F). Larimer Co., 7 mi. S of Fort Collins, 3 May 1965, *Irving 6511* (TEX). Las Animas Co., N of Mesa de Maya, 28 Apr. 1948, *Rogers 5664* (COLO, TEX). Lincoln Co., 2.5 mi. E of

Lincoln, 7 May 1987, *Falb & Miercort 23A* (RM). Moffat Co., Blue Mountain, 8.2 mi. N of U.S. Hwy. 40, 6.5 airline mi. NNE of Dinosaur, 11 June 1971, *Holmgren et al. 5162* (CAS, NY, US, WTU). Park Co., Como, 15 June 1892, *Hughes 42* (GH). Saguache Co., 2 mi. S of Villa Grove on U.S. Hwy. 285, 27 May 1968, *Turner 5774* (TEX). Weld Co., Pawnee Buttes, 1 July 1906, *Dodds 2111* (COLO). **Montana:** Big Horn Co., road to visitor center at Yellowtail Dam, 16 May 1983, *Lichvar 5666* (RM). Blaine Co., Chinook, 26 May 1937, *Wellington 1049* (MONTU). Carter Co., Medicine Rocks State Park, 28 Apr. 1986, *Mooers et al. 1085* (MONTU). Cascade Co., ca. 14 mi. W of Great Falls, 11 May 1956, *Booth 56224* (GH, MONTU). Chouteau Co., Fort Benton, June 1883, *Anderson 547* (US). Custer Co., 5 *Woolfolk* 1936 (GH, PH, POM, RM). Daniels Co., *Von Kuster 12* (RM). Dawson Co., 5 mi. SW of Glendive, 20 May 1965, *McMullin 308* (UC). Fergus Co., 3 mi. up Fords Creek turn off, 19 May 1988, *Lipscomb 1* (MONTU). Gallatin Co., bench gravel, 6 July 1910, *Spragg 245* (MONTU). Garfield Co., 15 mi. N of Jordan, 13 May 1968, *Woodland 1632* (CAS). Glacier Co., S of Hudson Bay Divide, 31 May 1958, *Harvey 66750* (MONTU). Judith Basin Co., Long's Ranch, 8 June 1900, *Wilcox 388* (US). Lewis and Clark Co., ca. 4 mi. W of Wolf Creek, 2 July 1948, *Hitchcock 17984* (CAS, COLO, GH, MONTU, NY, POM, UC, WS). McCone Co., Wolf Point, 19 May 1937, *Buck-of 546* (MONTU, WTU). Musselshell Co., Roundup, 11 May 1937, *Syblon 522* (CAS, RM, UC, WTU). Petroleum Co., Flatwillow, 28 May 1936, *Wickland 18* (MONTU). Powder River Co., 18 May 1975, *Lackschewitz 5937* (MONTU). Prairie Co., 10 mi. S of Brockway, 5 May 1941, *Koch 4* (MONTU). Rosebud Co., along U.S. Hwy. 212, ca. 10–15 mi. W of Ashland, 18 July 1967, *Hess 762* (MO). Sheridan Co., Westby, 17 July 1927, *Larsen 20* (GH, MO, PH, RM). Sweet Grass Co., Big Coulee Creek, *Blankinship* 1902 (MONTU, WS, WTU). Teton Co., 22 mi. SW of Chouteau, *Finley* 1963 (MONTU); Collins, *Jones* 1904 (UC). Toole Co., Sweetgrass, *Recup* 1918 (NY). Valley Co., Fork Peck, 26 May 1919, *Ramsden & Lackschewitz 345* (MONTU). Wibaux Co., Hodges, *Griffins* 1936 (MONTU, RM, TEX, WTU). Yellowstone Co., 10 mi. NW of Billings on Lavina Road, 3 June 1973, *Doles 563* (UT). **Nebraska:** Box Butte Co., Hemingford, 1 June 1950, *Kiener 24623* (US). Cheyenne Co., 2 mi. W of Sunol, 18 May 1970, *Stephens 38111* (NCU). Deuel Co., Rush Creek, *Rydberg* 1891 (GH, US). Keith Co., E of Cedar Point Biological Station, 7 June 1983, *Sutherland 5598* (NY). Kimball Co., 8 mi. SW and 1.5 mi. S of Bushnell, 18 May 1970, *Stephens 38143* (GH, NY). Garden Co., Ash Hollow State Park, W of Lewellen on U.S. Hwy. 26, 19 May 1976, *Churchill 7323* (MO, NY). Sheridan Co., 13 mi. N of Hay Springs, 5 May 1964, *Nixon 6* (RM). Sioux Co., 7.5 mi. S of the junction of Nebraska Hwys. 2 & 71 on Hwy. 71, 27 May 1972, *Churchill 77* (MO, NY). **New Mexico:** Union Co., Capulin Mountain National Monument, 17 July 1941, *A. & R. A. Nelson 4650* (MONTU). **North Dakota:** Billings Co., Cedar Canyon, 9 June 1952, *Clausen 8194* (GH). Burleigh Co., Bismarck, *Lanterman* 1891 (MO, NY, WTU). Burke Co., Portal, 18 June 1903, *Barber 360* (GH). Divide Co., 25 May 1961, *Stevens 2377* (UC, US). Dunn Co., Killdeer Historical Site, *Stevens* 1951 (US). Grant Co., Pretty Rock National Wildlife Refuge, 23 Aug. 1907, *Bell 1197* (UC). Mercer Co., Missouri River Valley, 8 mi. N of Knife River, 29 June 1941, *Stevens 905* (NCU, UC, US). Morton Co., Glen Ullin, May 1891, *Holzinger 5* (GH). Mountrail Co., 12 July 1960, *Stevens & Moir 2289* (NCU, UC). Slope Co., *Atkinson* 1935 (F, NCU, RM, UC). Stark Co., Dickinson, *Whitman* 1949 (US). Ward Co., *Haigh* 1900 (NY). Williams Co., Williston, *Stevens* 1918 (F). **Oklahoma:** Cimarron Co., N of Mesa, 28 Apr. 1948, *Rogers 5664* (US). **South Dakota:** Butte Co., 5 mi. N of Belle Fourche, 23 May 1970, *Stephens 38357* (NY). Custer Co., head of Blocktail Gulch, 12 Apr. 1910, *Murdoch 4020* (F, NY). Fall River Co., Ochich, 8 Apr. 1911, *Nelson 2724* (F, RM). Jackson Co., Cedar Pass, 17 July 1913, *Over 6113* (COLO). Harding Co., 4 Aug. 1927, *Over 17438* (US); Rabbit Butte, 1 May 1912, *Vesher 553* (F). Lawrence Co., near Lead, 17 June 1929, *Palmer 37352* (GH, MO, NY, US). Meade Co., 40 mi. NW of Rapid City, 9 July 1947, *Crider & Atkins 44* (RM). Pennington Co., Black Hills, Harney Peak, 8 July 1927, *Hayward 1961* (F, RM). Perkins Co., Lemmon, *Halse* 1969 (OSC). **Utah:** Daggett Co., 6 air mi. N of Dutch John, 7 June 1979, *Atwood 7284* (NCU). Uintah Co., ca. 14 air mi. NW of Vernal along Tridell–Dry Fork Road, 31 June 1983, *Neese 14116* (MONTU, NY). **Wyoming:** Albany Co., Laramie Mts., Telephone Canyon, 30 May 1936, *Ownbey 1027* (COLO, MO, MONTU, RM, WS, WTU). Campbell Co., ca. 8 air mi. SE of Reno Junction at Little Thunder Creek, 3 June 1978, *Hartman & Dueholm 5896* (NY, RM). Carbon Co., Como Bluff, 25 May 1947, *Porter 4162* (CAS, MO, NY, PH, RM, TEX, UC, WTU). Converse Co., near the head of La Prele Creek, 27 June 1950, *Porter 5374* (CAS, COLO, GH, MO, NY, RM, TEX, WTU). Crook Co., 8 mi. NW of Hulett, 6 June 1935, *Ownbey 646* (COLO, MO, MONTU, NY, RM, UC, WS, WTU). Fremont Co., ca. 20 mi. SW of Lander along Wyoming Hwy. 28, 2 July 1983, *Evert 5282* (NY, RM). Goshen Co., sandy hills between Wheatland and Veteran, 19 June 1953, *Porter 6235* (RM, WTU). Hot Springs Co., 20 mi. NW of Thermopolis along Wyoming Hwy. 120, 3 July 1983, *Evert 5312* (NY, RM). Johnson Co., Bighorn Mts. W of Buffalo, Circle Park, 23 July 1958, *C. L. & M. W. Porter 7562* (CAS, RM, UC, WTU). Laramie Co., Pine Bluffs, 2.5 mi. S of U.S. Hwy. 30 and Interstate Hwy. 80, 6 June 1969 *Cox & Dunn 1091* (MO). Natrona Co., 5 mi. W of Powder River, 5 July 1979, *Dueholm 7760* (NY, RM). Niobrara Co., 22.5 air mi. NW of Lusk and 14.5 air mi. SW of Lance Creek, 2 June 1978, *Nelson 1591* (RM). Platte Co., 21.5 air mi. N of Guernsey, 31 May 1978, *Nelson 1540* (NY, RM, UC). Sheridan Co., 9 mi. S of Sheridan, 30 June 1979, *Dueholm 7542* (NY, RM). Sweetwater Co., 16 mi. W of Wyoming Hwy. Rt. 789, 15 July 1973, *Hill 985* (RM). Washakie Co., S of Ten Sleep, 25 July 1901, *Goodding 353* (F, GH, MO, NY, RM, US). Weston Co., 3.5 air mi. NW of Osage, 22 May 1984, *Marriott 6214* (NY, RM).

Larisey (1940) accepted three varieties under this species, but all of them were reduced to *Thermopsis rhombifolia* var. *rhombifolia* by Isely (1981). Although Isely's treatment extended the parameters of *Thermopsis rhombifolia* to include the long-recognized species *T. montana* and *T. divaricarpa*, which we do not accept, we agree that recognition of varieties within our narrower concept of *T. rhombifolia* is not justified. *Thermopsis rhombifolia* does not appear to intergrade with

either *T. divaricarpa* or *T. montana*, but the occasional hybrid or hybrid swarm is believed to occur between at least *T. rhombifolia* and *T. divaricarpa*, especially in Albany County, Wyoming. The name *T. arenosa* is probably based on such hybrid variants (see discussion under *T. divaricarpa*).

9. Thermopsis robusta Howell, Erythea 1: 109. 1893. TYPE: U.S.A. California: "California Coast Range, near the Oregon boundary," *T. Howell* 1884 (holotype, ORE; isotypes, F, GH, NY [2 sheets], US, WS, WTU).

Some of the apparent isotypes are labeled "Coast Mts., Curry Co., Oregon" (GH) and "Oregon, Coast Mountains, fortieth parallel" (F, NY, US, WTU), while another is labeled "Oregon, Coast Mountains, forty-second parallel" (WS). We have accepted the location as given in the protologue (above), which would place the actual type locality in California, probably Humboldt or Siskiyou County to judge from the specimens we have examined.

Plants robust, 8–18 dm tall, densely tomentose; stems thick, erect, clustered, well-branched, arising from a woody rootstock; branches ascending at 30–50°, strongly zigzagged. Leaflets elliptic to widely elliptic or ovate, 6.5–11 cm long, 2.5–6.5 cm wide, acute to acuminate, short mucronate, tomentose, lateral veins 9–12 pairs, not conspicuously net-veined beneath; petioles 2.2–3.5 cm long; stipules persistent, widely ovate to nearly lanceolate, 1.5–5.5 cm long, 0.7–3 cm wide, oblique to cuneate, acuminate. Racemes 20–45 cm long, with 20–40 flowers, in whorls of 2–5 or scattered; peduncles 7–10 cm long; pedicels 4–8 mm long, densely tomentose; bracts persistent, ovate, 8–14 mm long, 3–8 mm wide. Flowers 1.6–1.8 cm long; calyx 7–9 mm long, 5–8 mm wide at the limb, lobes 2–4 mm long, as long as or shorter than tube; wing and keel petals asymmetrically oblong-rhombic; ovary densely tomentose; ovules 10–13. Pods arcuate, divergent, 4.5–6.5 cm long, 0.4–0.5 cm wide, densely tomentose. Seeds 5–10, brown, reniform without a rostrum, 3.5–4 mm long, 2 mm wide.

Distribution and ecology (Fig. 1). Known only from northwestern California, Humboldt and Siskiyou cos., along ridgetops, 150–1500 m; flowering May–June.

Specimens examined. U.S.A. **California:** Humboldt Co., ca. 12 mi. SW of Orleans, Bee Mt., *Quick 59-42* (CAS, COLO, TEX); 11 mi. from Orleans on Bar Shanty Road, 6 July 1956, *Tillett 620* (POM); E of Korbel, Bald Mt., on trail to Blohn's cabin, June 1951, *Vollmer & Beane 146* (CAS, POM, WTU); near Orleans, 19 May 1931, *Wieslander 7* (RM, UC). Siskiyou Co., 11 mi. N of Somes Bar, shady forest near Camp Three, 22 June 1954, *Hitchcock 20223* (NY, WTU); 9.5 mi. N of Klamath River, Cedar Camp Road, 11 July 1950, *Hoffman 3643* (UC); Prospect Hill, 1220 m, 18 July 1950, *Tracy 19220* (UC); Prospect Hill, 20 July 1950, *Tracy 19213* (POM, UC, WTU); near State Creek, 12 June 1928, *Wieslander 129* (JEPS). County unknown, coast of California, *Vasey* 1876 (GH).

Thermopsis robusta is a localized, robust endemic of northwestern California. Because of its habit, large leaflets, and densely pilosulous vestiture it is superficially similar to *T. macrophylla*. Both Larisey (1940) and Isely (1981) included *T. robusta* within their concept of *T. macrophylla* var. *macrophylla*. We believe it is more closely related to *T. gracilis*, to judge from its divergent pods and distribution.

10. Thermopsis villosa (Walter) Fernald & B. G. Schubert, Rhodora 50: 201. 1948. *Sophora villosa* Walter, Fl. Carol. 134. 1788. TYPE: U.S.A. North Carolina: without definite locality or date, *Walter s.n.* (holotype, BM not seen). Typification of this plant is thoroughly discussed by Fernald & Schubert in their transfer of the species from *Sophora* to *Thermopsis*.

Thermopsis caroliniana M. Curtis, Amer. J. Sci. 44: 80. 1843. TYPE: U.S.A. North Carolina: Haywood Co., "in sylvis montanis," *M. A. Curtis* 1839 (holotype, GH; possible isotypes, PH, NY).

Plants delicate, 6–18 dm tall, glabrate (densely villous inflorescences); stems thick, erect, solitary or clustered, few-branched, arising from a woody rootstock; branches spreading at 45–60°, moderately zigzagged. Leaflets elliptic, 4–9.5 cm long, 1.8–4.4 cm wide, acute to obtuse, glabrate above, sparsely villous below, lateral veins 6–8 pairs, conspicuously net-veined beneath; petioles 2–5(–6) cm long; stipules persistent, elliptic to ovate, 1.5–4.5 cm long, 0.9 to 2.4 cm wide, oblique to cuneate, acute to obtuse. Racemes 15–50 cm long, with 10–50 flowers, scattered or in whorls of 2–3; peduncles 6–13 cm long; pedicels 2–3 mm long, densely villous; bracts deciduous, widely ovate to widely obovate, 5–7 mm long, 5–6(–8) mm wide. Flowers 1.7–1.9 cm long; calyx 7–8 mm long, 5–6.5 mm wide at the limb, lobes 2–3 mm long, much shorter than tube; wing and keel petals asymmetrically oblong-rhombic; ovary velutinous; ovules 12–16. Pods straight to slightly arcuate, erect, 4–5.5 cm long, 0.4–0.6 cm wide, densely tomentose to villous. Seeds 7–12, olive brown, elliptic with a

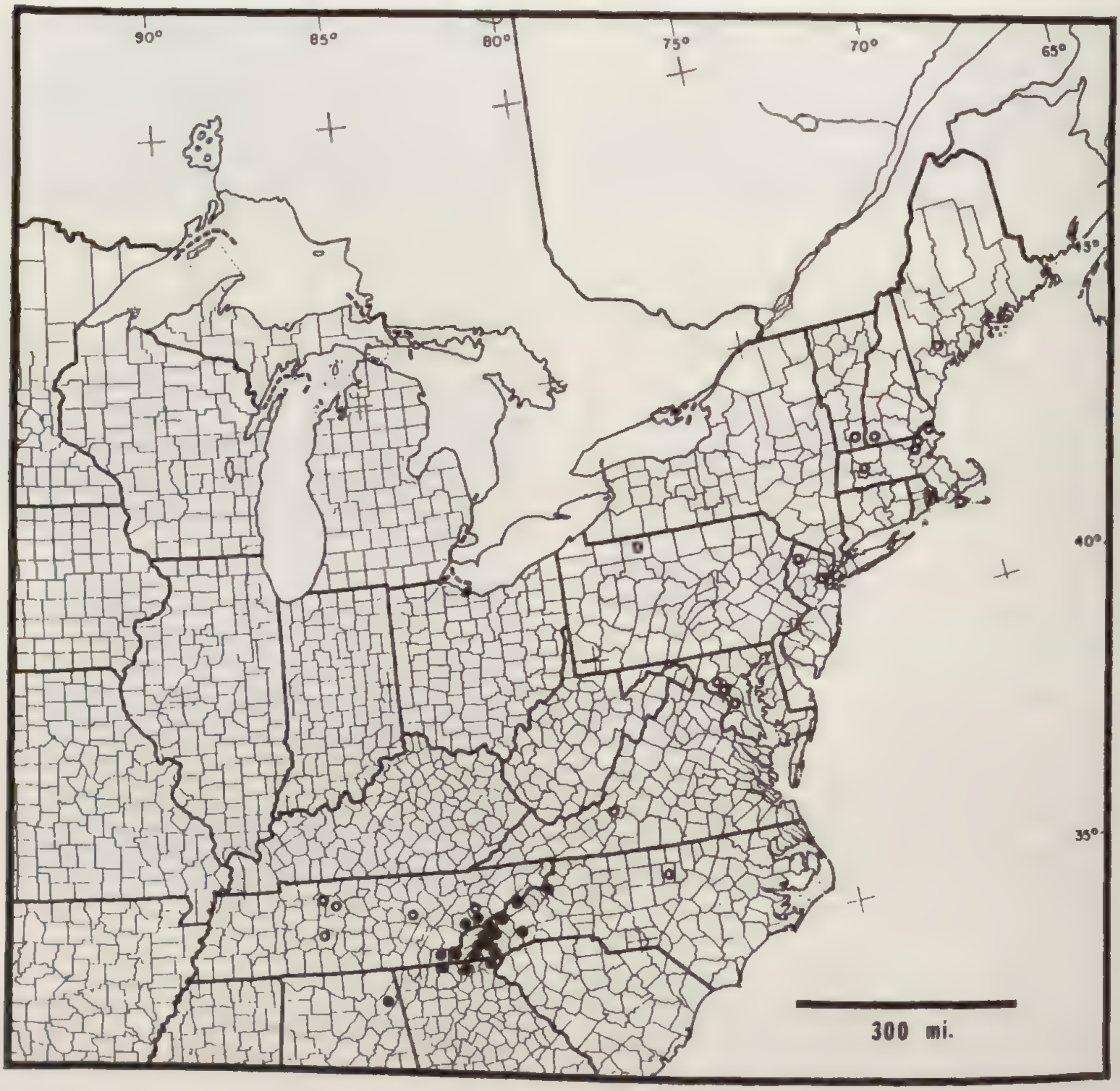

FIGURE 8. Distribution of *Thermopsis villosa*: collections thought to be native (closed circles); collections thought to be introduced or cultivated (open circles).

rostrum, 3–3.5 mm long, 1.8–2 mm wide. Chromosome number, $2n = 18$.

Distribution and ecology (Fig. 8). Native to eastern Tennessee, western North Carolina, northeastern Alabama, northern Georgia, and closely adjacent South Carolina, cultivated northward to Maine, scattered localized populations in open areas of deciduous oak woodlands, mostly 1000–1600 m; flowering May–June(–July).

Representative specimens examined. U.S.A. **Alabama:** DeKalb Co., 6 mi. N of Dawson, 2 July 1943, *Harper 3941* (F, GH, MO). **Georgia:** Fannin Co., near Three Forks Mountain, 28 June 1983, *Coile et al. 3736* (RM), 23 July 1909, *Smith 2475* (F). Rabun Co., Tallulah River, *Small* 1893 (F, GH, MO, NY, PH, UC, US). Union Co., Brasstown Bald Mt., 15 July 1908, *Howell 393* (US). **Maine:** Hancock Co., Reef Point Gardens, *Spaulding 582* (GH). **Maryland:** Prince Georges Co., *Hermann 18409* (RM). **Massachusetts:** Hampshire Co., Northampton, railroad right-of-way, *Ahles 78850* (TENN). Middlesex Co., Framingham, Pike exit to Massachusetts Hwy. 9, 27 June 1975, *Ahles 80370* (NEBC); Wilmington, W side of Interstate Hwy. 93, 22 June 1986, *Boufford & Wood 23650* (CAS, NEBC, MO, PH). **New Hampshire:** Cheshire Co., *Boufford 6134* (MO). **New Jersey:** Sussex Co., *Edwards* 1971 (NCU). Union Co., *Moldenke et al. 30109* (ARIZ, LL). **North Carolina:** Avery Co., 0.5 mi. N of Cranberry on U.S. Hwy. 19E, 17 June 1958, *Ahles & Duke 43574* (NCU). Cherokee Co., Notley River near North Carolina Hwy. 60, 6 June 1953, *Radford & Haesloop 7187a* (NCU); *Rugel* 1842 (NY). Clay Co., base of Doe Knob, Buck Creek, 24 July 1951, *Godfrey 51485* (TENN, US); NE of Chunky Gal Mt., along Buck Creek Road, 26 June 1970, *Leonard et al. 3314* (NCU). Haywood Co., 1.6 mi. N of Cove Creek, 5 June 1958, *Ahles & Duke 42242* (NCU). Henderson Co., ca. 1 mi. N of Lake Logan, 12 June 1964, *Wilbur 7142* (GH, UC). Jackson Co., near Soco Falls, 6 July 1940, *Hood 109* (MO); Soco Gap, ca. 3 mi. W of U.S. Hwy. 19, 1 July 1954, *Sargent 6851* (POM, RM, WTU). Macon Co., near Highlands, *Biltmore Herbarium 1332b* (F, GH, MO, NCU, NY, US); 3 mi. SE of Sassafras

Gap, 18 June 1969, *Leonard & Russ 2512* (COLO, NCU, POM, TENN, UC, WTU); 6.7 mi. W of Wayah Valley Ranch, Arrowood Glade, 29 June 1970, *Turner 6072* (F, GH, NY, RM, TEX, WTU). Madison Co., *Ahles & Duke 46380* (NCU, NY). Swain Co., along stream, 12 June 1982, *Churchill 82698* (RM); 1.3 mi. from North Carolina Hwy. 28 on Mica Knob Road, 6 June 1956, *Bell 3200* (GH, NCU). Transylvania Co., U.S. Hwy. 276 near Pink Beds, 23 Sep. 1957, *Freeman 57819* (NCU); along motor road in Pink Beds, *Ripper 307* (RM). **Pennsylvania:** McKean Co., *Fogg & Wherry 9818* (PH). **Tennessee:** Blount Co., Cades Cove, near Crib Gap, *Hoss* 1954 (TENN). Cumberland Co., *Adams* 1962 (NCU, TENN, US). Davidson Co., NW Nashville, at intersection of Marrowbone and Eaton's Creek Roads, 17 June 1968, *Kral 31489* (NCU, TENN). Maury Co., just S of and above Rockdale on U.S. Hwy. 43, 26 June 1970, *Kral 39741* (GH, MO, NY); Harpeth hills near Nashville, *Gattinger* 1879 (GH, MO, NY, US). Polk Co., ca. 1.5 km SE of summit of Big Frog Mt., 14 July 1983, *Z. E. & J. B. Murrell 389* (TENN). **Vermont:** Windham Co., *Charette 3345* (MO), *and 3349* (NEBC). **Virginia:** Roanoke Co., *Uttal 6228* (NCU).

Thermopsis villosa is a distinctive, stiffly erect species of the southern Appalachian ridges and upper valleys. Czefranova (1970) treated it (as *T. caroliniana*) as the only member of series Carolinianae. It is superficially similar to the Californian *T. macrophylla*, as noted by Gray (1848a), in having densely villous inflorescences and closely compacted erect pods but differs markedly from that species in its much more slender, strict habit and glabrate foliage.

Sporadic, locally naturalized populations of this taxon occur from Virginia, northeastward to Maine. Fernald (1950) did not account for *T. villosa* in his treatment of *Thermopsis* for the northeastern United States, nor did he comment on the clearly naturalized populations of this species outside of its natural distribution (Fig. 8).

The species was taken into cultivation early on. Gray (1848a) stated "I raised the plant in the Cambridge Botanic Garden (where it is perfectly hardy) from seeds . . . communicated by Mr. Buckley." No doubt the species is still retained in the occasional garden or has persisted in gardens long vacated. One collection is known from Hawaii (Oahu, "Mauka of Kawaiiki ditch intake," 30 Apr. 1939, *Degener 17363*, GH). We also believe that the numerous collections near Nashville, first made by Gattinger in the Harpeth hills in 1875 (MO, TENN, US), may also be locally naturalized populations.

Literature Cited

Abrams, L. 1944. Fabaceae. Pp. 480–627 *in* An Illustrated Flora of the Pacific States, Washington, Oregon, and California, Vol. 2. Stanford Univ. Press, Stanford, California.

Alston, R. E. & B. L. Turner. 1963. Natural hybridization among four species of *Baptisia* (Leguminosae). Amer. J. Bot. 50: 159–173.

Balandrin, M. F., E. F. Robbins & A. D. Kinghorn. 1982. Alkaloid distribution in some species of the Papilionaceous tribes Thermopsideae and Genisteae. Biochem. Syst. & Ecol. 10(4): 307–311.

Bisby, F. A. 1981. Genisteae (Adans.) Benth. Pp. 409–425 *in* R. M. Polhill & P. H. Raven (editors), Advances in Legume Systematics. Royal Botanic Gardens, Kew.

Brewer, W. H. & S. Watson. 1880. Polypetalae. *In:* Botany of California, Vol. 1. Welch, Bigelow, Cambridge, Massachusetts.

Brown, R. 1811. P. 3 *in* W. T. Aiton (editor), Hortus Kewensis, ed. 2, Vol. 3. Longman, Hurst, Rees, Orme & Brown, London.

Chen, C. J., X. Y. Zhu & Y. M. Yuan. 1992. Cytological studies on the tribe Thermopsideae (Fabaceae) I. Report on karyotypes of eleven species of four genera. Cathaya 4: 103–116.

Cranmer, M. F. & B. L. Turner. 1967. Systematic significance of lupine alkaloids with particular reference to *Baptisia* (Leguminosae). Evolution 21: 508–517.

Cristofolini, G. 1987. Serological relationships among Sophoreae, Thermopsideae, and Genisteae (Fabaceae). Bot. J. Linn. Soc. 94: 421–432.

——— & L. Feoli-Chiapella. 1984. Origin and diversification of the Genisteae. Webbia 38: 105–122.

Czefranova, Z. 1970. Series novae generis *Thermopsis* R. Br. Novitates Systematicae Plantarum 7: 213–216.

Dement, W. A. & T. J. Mabry. 1975. Biological implications of flavonoid chemistry in *Baptisia* and *Thermopsis*. Biochem. Syst. & Ecol. 3: 91–94.

Faugeras, C. & R. Paris. 1968. Chemiotaxinomie des Papilionacées–Genistées. Bull. Soc. Bot. France 1965: 75–102.

Federov, A. A. (editor). 1969. Chromosome Numbers of Flowering Plants. Acad. Sci. USSR, Moscow.

Fernald, M. L. 1950. Gray's Manual, 8th ed. American Book Company, New York.

Gillett, J. M. 1975. *In:* A. Löve (editor), IOPB Chromosome Number Reports L. Taxon 24: 671–678.

Graustein, J. E. 1967. Thomas Nuttall, Naturalist, Explorations in America, 1808–1841. Harvard Univ. Press, Cambridge.

Gray, A. 1848a. Chloris Boreali-Americana. Mem. Amer. Acad. Arts n.s. 3(1): 1–56.

———. 1848b. A Manual of the Botany of the Northern United States. James Monroe, Boston.

Greuter, W., et al. 1988. International Code of Botanical Nomenclature. Regnum Veg. 118.

Harborne, J. B. 1969. Chemosystematics of the Leguminosae. Flavonoid and isoflavonoid patterns in the tribe Genisteae. Phytochemistry 8: 1449–1456.

Howell, J. T. 1957. The Santa Ynez *Thermopsis*. Leafl. W. Bot. 7(6): 158–159.

Isely, D. 1978. New varieties and combinations in *Lotus*, *Baptisia*, *Thermopsis*, and *Sophora* (Leguminosae). Brittonia 30: 466–472.

———. 1981. Leguminosae of the United States, III. Subfamily Papilionoideae: Tribes Sophoreae, Podalyrieae, and Loteae. Mem. New York Bot. Gard. 25(3): 1–264.

Larisey, M. M. 1940. A revision of the North American

species of the genus *Thermopsis*. Ann. Missouri Bot. Gard. 27: 245–258.

LEDINGHAM, G. F. 1957. Chromosome numbers of some Saskatchewan Leguminosae with particular reference to *Astragalus* and *Oxytropis*. Canad. J. Bot. 35: 657–666.

LINK, H. F. 1821. Icones Plantarum Selectarum. Published by the author, Berlin.

LINNAEUS, C. 1753. Species Plantarum, ed. 1. Holmiae [Stockholm], (impensis Laurentii Salvii).

LÖVE, A. & D. LÖVE. 1982. *In:* A. Löve (editor), IOPB Chromosome Number Reports LXXV. Taxon 31: 342–368.

MESICEK, J. & J. SOJAK. 1969. Chromosome counts of some Mongolian plants. Folia Geobot. Phytotax. 4: 55–86.

NUTTALL, T. 1818. The Genera of North American Plants. Printed for the author by D. Heart, Philadelphia.

POLHILL, R. M. 1976. Genisteae (Adans.) Benth. and related tribes (Leguminosae). Pp. 143–368 *in* V. H. Heywood (editor), Botanical Systematics, Vol. 1. Academic Press, New York.

PROBATOVA, N. S. & A. P. SOKOLOVSKAYA. 1981. Kariologicheskoe issledovanie sosudistykh rastenij ostrovov Dal'nevostocnogo gosudarstvennogo morskogo sapovednika. Sb. Cvetkaye Rastenija Ostrovov Dalnevostochnogo Morskogo Sapovednika. Pp. 92–114.

RADFORD, A. E., H. E. AHLES & C. R. BELL. 1968. Manual of the Vascular Flora of the Carolinas. Univ. North Carolina Press, Chapel Hill, North Carolina.

RAFINESQUE, C. S. 1819. J. Phys. Chim. Hist. Nat. Arts. 89: 259.

SALATINO, A. & O. R. GOTTLIEB. 1980. Quinolizidine alkaloids as systematic markers of the Papilionoideae. Biochem. Syst. & Ecol. 8: 133–147.

——— & ———. 1983. Chemogeographical evolution of quinolizidines in Papilionoideae. Pl. Syst. Evol. 143: 167–174.

SHISHKIN, B. K. 1945. *Thermopsis*. Pp. 30–36 *in* V. L. Komarov (editor), Flora of the USSR, Vol. 11. [English translation.] Israel Program for Scientific Translation. Jerusalem. 1971.

ST. JOHN, H. 1941. Notes on North American *Thermopsis*. Torreya 41: 112–115.

TAYLOR, R. L. 1967. *In:* A. Löve (editor), IOPB Chromosome Number Reports XIII. Taxon 16: 445–461.

TORREY, J. 1857. Explorations and surveys for a railroad. Pacific Railroad Rep. 4: 81.

———. 1859. Botany of the boundary. *In:* W. H. Emory (editor), Rep. U.S. Mex. Bound. Surv., Vol. 2, pt. 1. A.O.P. Nicholson, Printer, Washington.

——— & A. GRAY. 1840. A Flora of North America. Wiley & Putnam, New York.

TURNER, B. L. 1967. Plant chemosystematics and phylogeny. Pure Appl. Chem. 14: 189–213.

———. 1981. Thermopsideae. Pp. 403–407 *in* R. M. Polhill & P. H. Raven (editors), Advances in Legume Systematics. Royal Botanic Gardens, Kew.

———. 1982. Review of: D. Isely, Leguminosae of the United States. III. Subfamily Papilionoideae: Tribes Sophoreae, Podalyrieae, Loteae. Syst. Bot. 7(3): 350–352.

WILBUR, R. L. 1963. The Leguminous plants of North Carolina. Technical Bulletin No. 151. North Carolina Agricultural Experiment Station. Raleigh, North Carolina.

WILLDENOW, C. L. 1799. Species Plantarum. Berlin (impensis G. C. Nauk).

YEH, M. S., H. YUASA & F. MAEKAWA. 1986. Chromosome numbers in the Leguminosae. Sci. Rep. Res. Inst. Evol. Biol. 3: 57–71.

ZHUKOVA, P. G. 1967. Karyology of some plants, cultivated in the Arctic-Alpine Botanical Garden. Pp. 139–149 *in* N. A. Arorin (editor), Plantarum Zonam Polarem Transportatio. II. Leningrad.

THE BOTANICAL WORKS OF PHILIPPI, FATHER AND SON, IN CHILE[1]

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ABSTRACT

Rodulfo Amando Philippi (1808–1904) was a leading figure in Chilean natural history, including botany. His son Federico Philippi (1838–1910) was a botanist during the same period and worked closely with him. We present an orientation to their works and the information available about them. Both Philippis collected widely in Chile; their principal field trips are summarized. The Philippis' material, including types, is deposited primarily at SGO, but numerous specimens were distributed to other herbaria. The identification of type material is frequently complicated by sparse label data and many duplicates; lectotypes remain to be selected for many names. Although both Philippis published widely in a variety of journals and languages, their descriptions of Chilean plants were published principally in Chilean journals.

Rodulfo Amando Philippi (1808–1904; Phil.; "Rodolfo," Stafleu & Cowan, 1983) was one of the most important scientists in the history of Chile. He was a key figure in the inventory and description of the country's natural richness, the development of education there, and the development of the collections and libraries of the Museo Nacional de Historia Natural. He was aided in these efforts by his son, Federico Enrique Eunom Philippi (1838–1910; F. Phil.). Their work spans 60 years during the time of Chile's greatest expansion of territory and development. As the leading field biologists of their day, one or both of the Philippis were the first to explore much of the country, which their predecessor Claudio Gay had surveyed only from Copiapó to Chiloé. The Philippis published more than 560 articles on the natural history of Chile (R. A. Philippi: ca. 453 articles; Federico: ca. 109 articles) in a variety of Chilean and European journals, mostly in Latin, Spanish, and German. These articles cover notably (but by no means exclusively) paleontology, avifauna, entomology, exploration, anthropology, minerals, marine mammals, molluscs, plants, and general observations of their numerous field trips. The Philippis, particularly R. A. Philippi, were highly regarded by their colleagues.

Of their various fields of interest, botany was foremost for both men. R. A. Philippi was prolific in both the field and the herbarium, and ultimately described 3720 new species of plants from Chile (Muñoz-Schick, 1973). Federico collected material that his father described; he himself described 33 new species of plants (listed by Gotschlich, 1910, and Gunckel, 1939), most in publications compiled by his father. He was the first head of the Sección Botánica of the Museo Nacional, where he curated specimens and compiled an updated catalog of Chilean plants (F. Philippi, 1881), and he followed his father as professor of botany at the University of Chile, and director of the Jardín Botánico at the Quinta Normal.

In addition to the large number of works published by the Philippis, much has been written about them and their work. Here we concentrate on the botanical aspects of the combined works, to orient contemporary botanists to some of the common difficulties encountered in interpreting the Philippis' work and indicate useful sources of further information. The most common problems remain sparse documentation on their specimens and the Philippis' very close collaboration, to the point that in later years even their individual handwriting became difficult to distinguish.

A BIOGRAPHICAL SKETCH

Detailed biographies have been published, most focussing on one or the other Philippi but documenting the lives of both by necessity (Barros-Arana, 1904; Gotschlich, 1904, 1910; Gunckel,

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1939; Muñoz-Shick, 1991). We present here a brief outline of both lives, with an emphasis on botanical activities.

R. A. Philippi was born just outside Berlin, and studied natural history in institutions in Switzerland and Berlin. He eventually obtained a medical degree but did not practice. He traveled widely in Europe as a young man, notably in Italy. Federico was born during his father's last stay in Naples (reportedly during an eruption of Vesuvius; Gotschlich, 1910). R. A. Philippi eventually settled into a teaching position in the newly established Polytechnic School in Kassel, where he spent 16 years. He published numerous articles from there, particularly on paleontology, molluscs, and the geology of southern Italy. He was widely known in the contemporary scientific community, and his works were recognized with medals from German and Italian rulers. However, he eventually found himself on the inconvenient side of a political upheaval in the duchy of Hesse, and left Kassel (precipitously and late on a cold December night; Barros-Arana, 1904). His brother was then organizing German colonization in southern Chile, and at his urging R. A. Philippi visited Chile. He arrived in Valparaíso in late 1851, in the midst of a civil war, and made his way south to the German colony near Valdivia. He made one exploring expedition inland in 1852, and then together with his brother acquired the Fundo ("Estate") San Juan along the Río Bueno.

Federico arrived in Chile in late 1853 with the rest of the family and his father's library. The family embarked in response to the father's decision to stay some time in Chile, and the news of his appointments in 1853 as director of the Museo Nacional de Historia Natural and as professor at the University of Chile. Here he taught natural history and wrote a textbook that presented ideas of evolution. But it was his exploring and collecting that developed the Museo Nacional into an active research center. This museum was established in 1830 by Claudio Gay, who deposited the collections that formed its basis when he left Chile in 1842. In 1876 R. A. Philippi moved the collections to their present site in the Quinta Normal de Agricultura, where the Jardín Botánico was later established.

R. A. Philippi lived in Santiago most of the year, visiting his family near Valdivia for two months in the summer and using much of this time for field studies. Federico remained with the family on the San Juan estate until his first wife's death in 1871, when he traveled to Europe to study botany and zoology. He returned in 1874 to take over his retiring father's teaching duties, and in 1889 became head of the newly established Sección Botánica of the Museo Nacional. In 1883, Federico also succeeded his father in the directorship of the Jardín Botánico, and in 1897 he resigned from both the Sección Botánica and the Jardín Botánico to succeed his father as director of the Museo Nacional. Following Federico's return from Europe, father and son lived together in Santiago, eventually on the grounds of the Jardín Botánico, and worked closely together.

Collecting Expeditions

Both Philippis were active field workers throughout their lives, even though both suffered health problems. R. A. Philippi visited Italy principally to improve his weak constitution; this apparently worked, for he was 82 years old when he undertook his walking trip from Concepción to Arauco. As a child Federico contracted meningitis, and he remained crippled by malformed legs and feet for the rest of his life.

Their principal expeditions and collecting efforts are outlined in Table 1. A detailed list of the names and precise locations, including latitude and longitude, of the Philippis' collecting localities has been presented previously by Muñoz-Pizarro (1960), Muñoz-Schick (1973), and Muñoz-Schick & Prina (1987). The scientific impact of the Philippis' discoveries has been discussed by Gunckel (1939). Some trips were undertaken by order of the government; for these a report was usually published by a government agency, in addition to the accounts sent to contemporary journals. It was not unusual for the Philippis to publish an account of the same trip in several different journals and to collaborate on the written accounts of trips made by one of them.

These trips brought discovery of many new and unusual phenomena. R. A. Philippi's 1852 trip around Osorno in the south produced some of the first maps of that region. His expedition in 1853–1854 to the Atacama desert was the first scientific exploring trip to that region, and he described presciently the difficulties later encountered in developing it as well as its lack of precious metals. In his 1864 trip through the Cordillera de la Costa near Valdivia, Federico Philippi visited the Cordillera Pelada, where he found a mountain range covered with a forest composed of millions of standing, long-dead *alerce* trees (*Fitzroya cupressoides* (Molina) Johnst., Cupressaceae), and also relictual pockets of Magellanic plant communities that were disjunct by hundreds of kilometers from their "nat-

TABLE 1. Principal travels of Rodulfo Amando Philippi and Federico Philippi in Chile. Precise locality information for most collecting sites can be found in Muñoz-Pizarro (1960), Muñoz-Schick (1973), and Muñoz & Prina (1987).

Dates	Travels
1852	R. A. Philippi; Río Bueno south of Valdivia, Volcán Osorno, Lago Llanquihue, Volcán Calbuco [X Region]
1853 (Nov.)–1854 (Feb.)	R. A. Philippi; by boat from Valparaíso to Coquimbo, by land to Copiapó, Atacama, Taltal (Atacama Desert) [V to II Regions]
1854–1856	R. A. & F. Philippi; various sites around Santiago and the adjacent Cordillera de los Andes [Metropolitan Region]
1858 (Dec.)	R. A. Philippi; Colonias del Sur [X Region]
1859 (Jan.–Mar.)	R. A. Philippi; Colonias del Sur [X Region]
1860	R. A. Philippi; Catemu [V Region], Laguna Ranco [X Region]
1860 (Jan.)	R. A. & F. Philippi; Fundo San Juan to La Unión, Daglipulli and adjacent Cordillera de los Andes, Lago Ranco [X Region]
1860 (late)	R. A. & F. Philippi, Quebrada de San Ramón [Metropolitan Region]
1862	R. A. Philippi; Nuevo Volcán de Chillán [VIII Region]
1863	R. A. Philippi; Nuevo Volcán and Baños de Chillán [VIII Region]
1864	R. A. Philippi; Juan Fernández Islands [V Region], Guayacán (Coquimbo) [IV Region]
1864 (Oct.)	F. Philippi; San Juan de los Cuncos, Cordillera de la Costa, Hueicolla, Cordillera Pelada [X Region]
1867	R. A. Philippi; Cauquenes [VII Region]
1875	R. A. Philippi; Ventisquero Cipreses [VI Region]
1875	F. Philippi; Laguna de Budi, Desembocadura (mouth) of Río Toltén [IX Region]
1877	R. A. Philippi; San Juan [X Region]
1877	R. A. & F. Philippi; Arauco, Malleco, Cautín, Cordillera de Nahuelbuta, Tres Piedras [VIII to IX Regions]
1878 (early)	F. Philippi; Termas de Chillán [VIII Region]
1878	R. A. Philippi; Coquimbo Province [IV Region]; Matanzas and Cahuil in Colchagua Province [VI Region]
1879 (early)	F. Philippi; Descabezado (headwaters) of Río Maule [VII Region]
1879 (early)	R. A. Philippi; Tomé, Quiriquina, Salto del Laja [VIII Region]
1880 (Jan.)	F. Philippi; east-central Chiloé, including Cucao and Ancud [X Region]
1880	R. A. Philippi; Isla Quiriquina (for fossils) [VIII Region]
1882	R. A. Philippi; Santa Rosa de Los Andes, Jahuel [V Region]
1883 (Jan.)	F. Philippi; Fray Jorge, mouth of Río Limarí, Baños del Toro [IV Region]
1883 (Mar.)	R. A. Philippi; Lebu, Arauco, Coronel [VIII Region]
1883 (Oct.)	R. A. Philippi; Curauma [V Region]
1884	F. Philippi; Valparaíso area including Concón and mouth of Río Aconcagua [V Region]
1884	R. A. Philippi; Valdivia, San Juan [X Region]
1885 (Jan.–Mar.)	F. Philippi, Carlos Rahmer (Subdirector and Preparator of the Museo Nacional), Pablo Ortega (Dissector of the Museo Nacional), Otto Philippi (grandson of R. A. Philippi and medical student); Valparaíso to Caldera by boat, to Copiapó by train, overland from Puerta de Paipote to Antofagasta de la Sierra, into Argentinian territory (Muñoz-Schick & Prina, 1987), San Pedro de Atacama, Laguna de Huasco, and Oasis de Pica [III to I Regions]
1885 (Sept.)	F. Philippi; Valparaíso to Caldera by boat, then overland along coast to Huasco [III Region]
1885	R. A. Philippi; Lebu, Arauco, Coronel, Renaico [VIII Region]
1886	R. A. Philippi; San Juan [X Region]
1887 (Apr.)	R. A. Philippi; Algarrobo [Metropolitan Region]

TABLE 1. Continued.

Dates	Travels
1887 (Nov.)	R. A. Philippi; Araucanía [IX Region
1888 (Jan.)	R. A. Philippi; Alfalfal [Metropolitan Region]
1889	R. A. Philippi; Baños Colina [Metropolitan Region]
1890	R. A. Philippi; Concepción to Arauco [VIII Region]
1891	R. A. Philippi; Victoria, Los Angeles, Curanilahue, Arauco, Valdivia [VIII to X Regions]
1891 (Oct.)	R. A. Philippi; Quilpué [V Region]
1892	R. A. Philippi; Baños Chillán [VIII Region]
1893 (Sept.)	F. Philippi, Filiberto Germain (Head, Sección Entomología, Museo Nacional); Fray Jorge [IV Region]
1893	R. A. Philippi; Concepción, Curanilahue [VIII Region]
1894	F. Philippi; Yerbas Buenas, Cahuil, Matanzas [VI Region]
1896 (Mar.)	R. A. Philippi; Constitución [VII Region]
1896–1908	F. Philippi; various trips to Valdivia, Fundo San Juan, Cautín, Constitución [VII to X Regions]

ural" range in the south. The Philippis' joint trip in 1877 to the Cordillera de Nahuelbuta explored territory recently wrested from the control of the Mapuche ("Araucano") Indians, and Federico's 1884 trip northward surveyed territory recently acquired during the war with Peru and Bolivia. Federico first noted several unusual plant communities, including an isolated southern population of *Araucaria araucana* (Molina) K. Koch (Araucariaceae) just north of the mouth of the Río Toltén and a relict Valdivian forest north of Santiago at Fray Jorge, in the semiarid region. The Philippis' extensive botanical collecting and knowledge enabled them to recognize these unusual plant distributions and provided the basis for much of our current knowledge of the Chilean flora.

THE PHILIPPIS' SPECIMENS

Most of the Philippis' Chilean material, including types, is deposited in the Museo Nacional de Historia Natural in Santiago (SGO). This material was variously collected and annotated by one or both Philippis. Collections of Chilean plants sent to the Philippis by others, notably Pearce, Volckmann, Solís de Ovando, Díaz, Landbeck, Fonck, Geisse, Juliet, Borchers, Germain, and King, were also incorporated into the SGO collection (Muñoz-Schick, 1991). All of these other collectors are identified on the sheets except Fonck, whose handwriting is distinctive (Fig. 1). There are duplicates of many collections, due to the ample material that was collected and Federico's maintenance of a personal herbarium at home. This personal collection contained duplicates of specimens deposited in the Museo Nacional. It was acquired by the Museo Nacional in 1911, after Federico's death; some of these specimens can be distinguished by their printed labels with black border and the legend "Herbarium Friderici Philippi" (Fig. 2; Muñoz-Schick, 1973: fig. 2). Many duplicate specimens were also distributed to other herbaria through gifts and exchange. This distribution had no particular system, and R. A. Philippi was noted for his enthusiasm and scientific generosity. Duplicate Philippi specimens from Chile are reported today to be found at BA, BAF, BM F, FI, G, K, L, LE, LZ, MA, P, SI, and W (Stafleu & Cowan, 1983), and are also found at CORD (Taylor, pers. obs.).

Samples of both Philippis' handwritings have been presented previously with commentary (Muñoz-Schick, 1973: figs. 1, 2) and are shown in Figure 2. Their handwriting was similar, and became more so as they aged. Although the collector of the specimen is frequently not noted, particularly on material originally deposited in the museum's collection, it can usually be determined by reference to the year and locality (Table 1).

The subsequent head of the Sección Botánica was Carlos (Karl) Reiche, who prepared a revised *Flora de Chile* (1894–1911). Reiche was familiar with the Philippis' specimens, and his commentary in this work is useful for selecting lectotypes. However, some of Federico's collections now in the Museo Nacional were purchased after Reiche's departure from Chile and were not seen by him. Reiche's handwriting is distinctive; his annotation consists usually of a single "R" (Fig. 3).

The types of species described by the Philippis are today housed in a separate collection. This was established by Muñoz-Pizarro when the specimens in the herbarium were mounted, a process that began in 1942 and continues today (Muñoz-Pizarro, 1960). Identification of Philippi types is sometimes difficult because of the sparse data on many specimens, the occasional inclusion of several collections on one sheet with no indication of which plant was accompanied by which label, and the frequent citation of more than one specimen in the

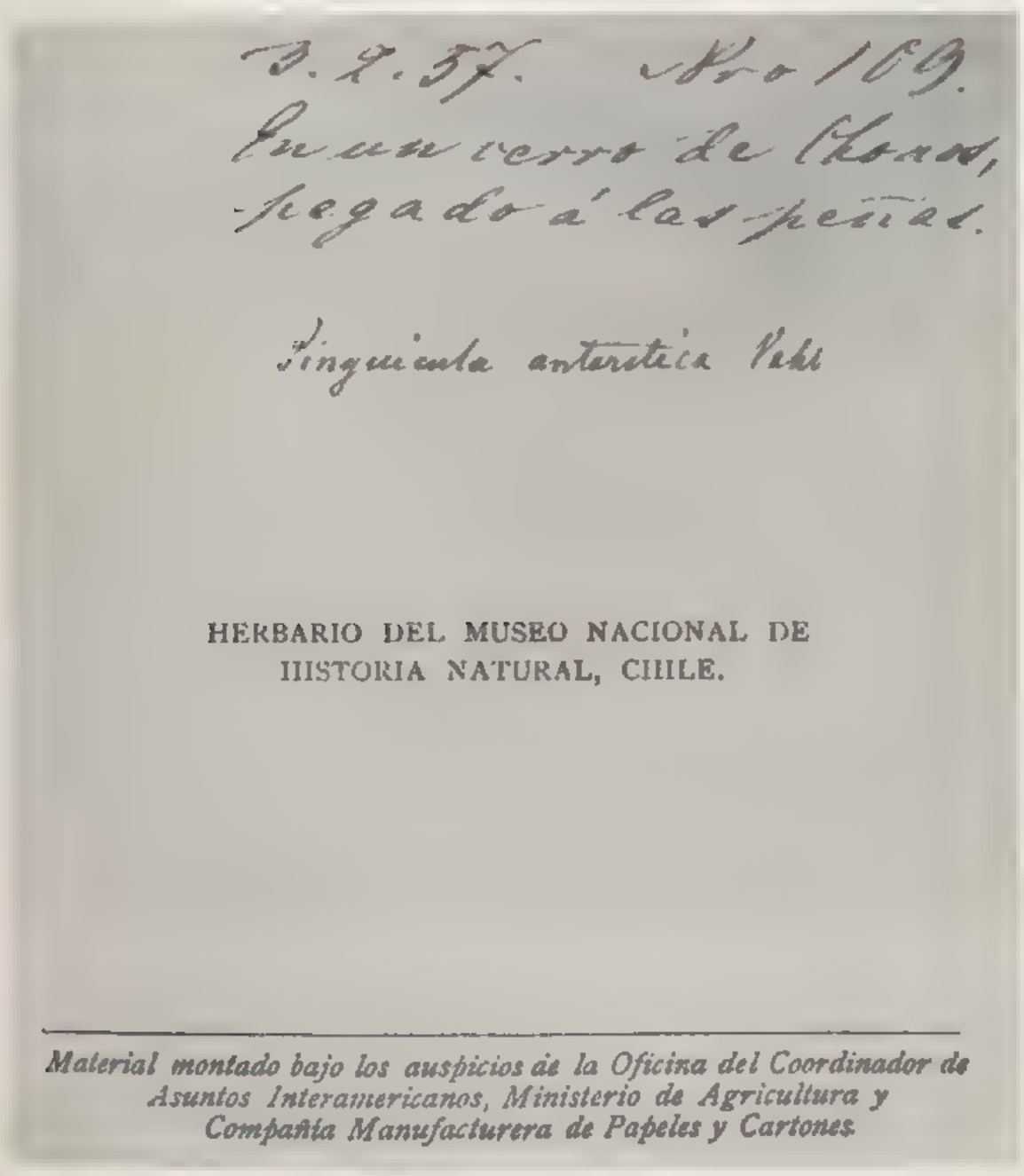

FIGURE 1. Handwriting samples: Collection data by Fonck (top portion) with annotation by R. A. Philippi (bottom portion).

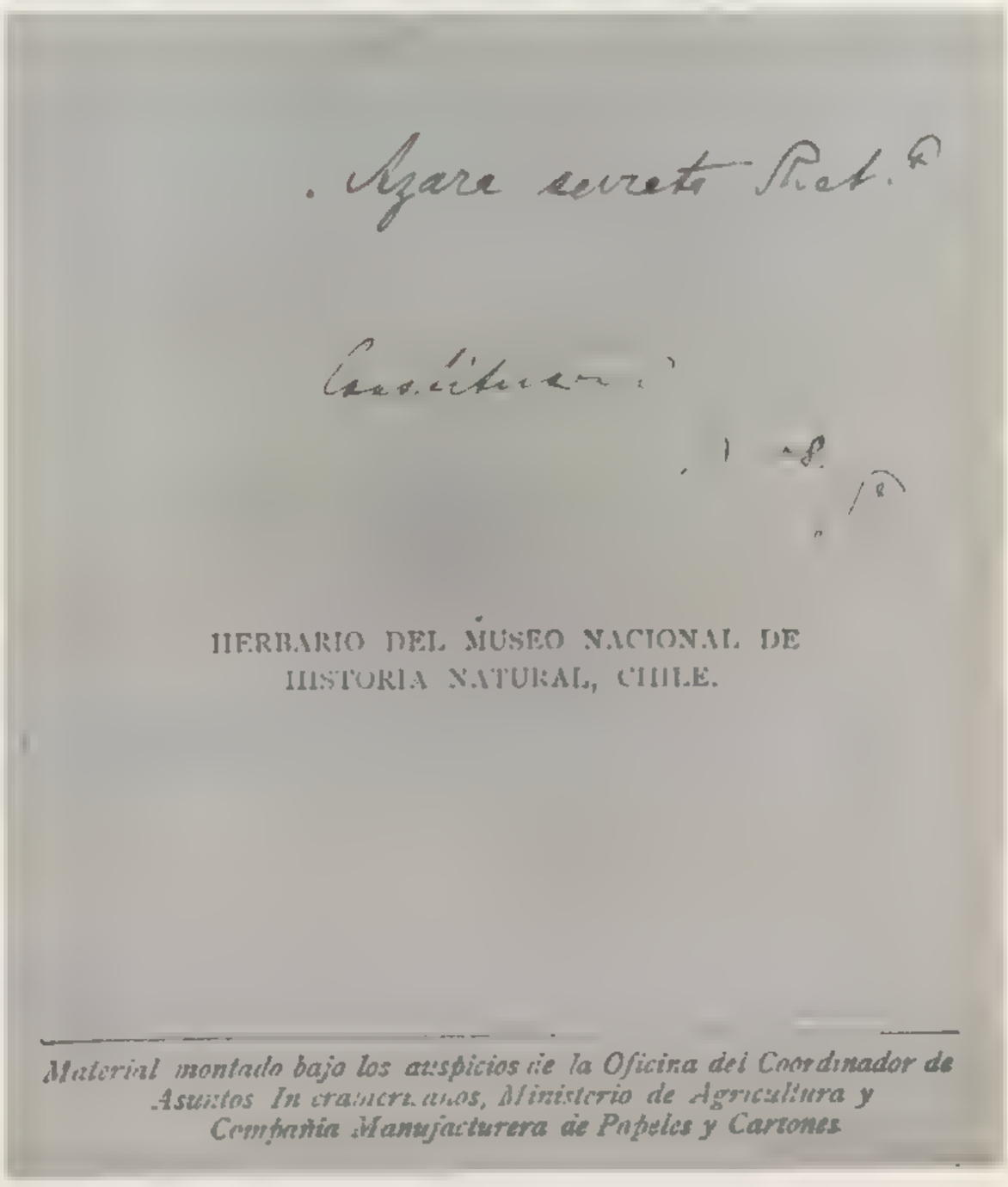

FIGURE 3. Handwriting sample: Label by Karl Reiche.

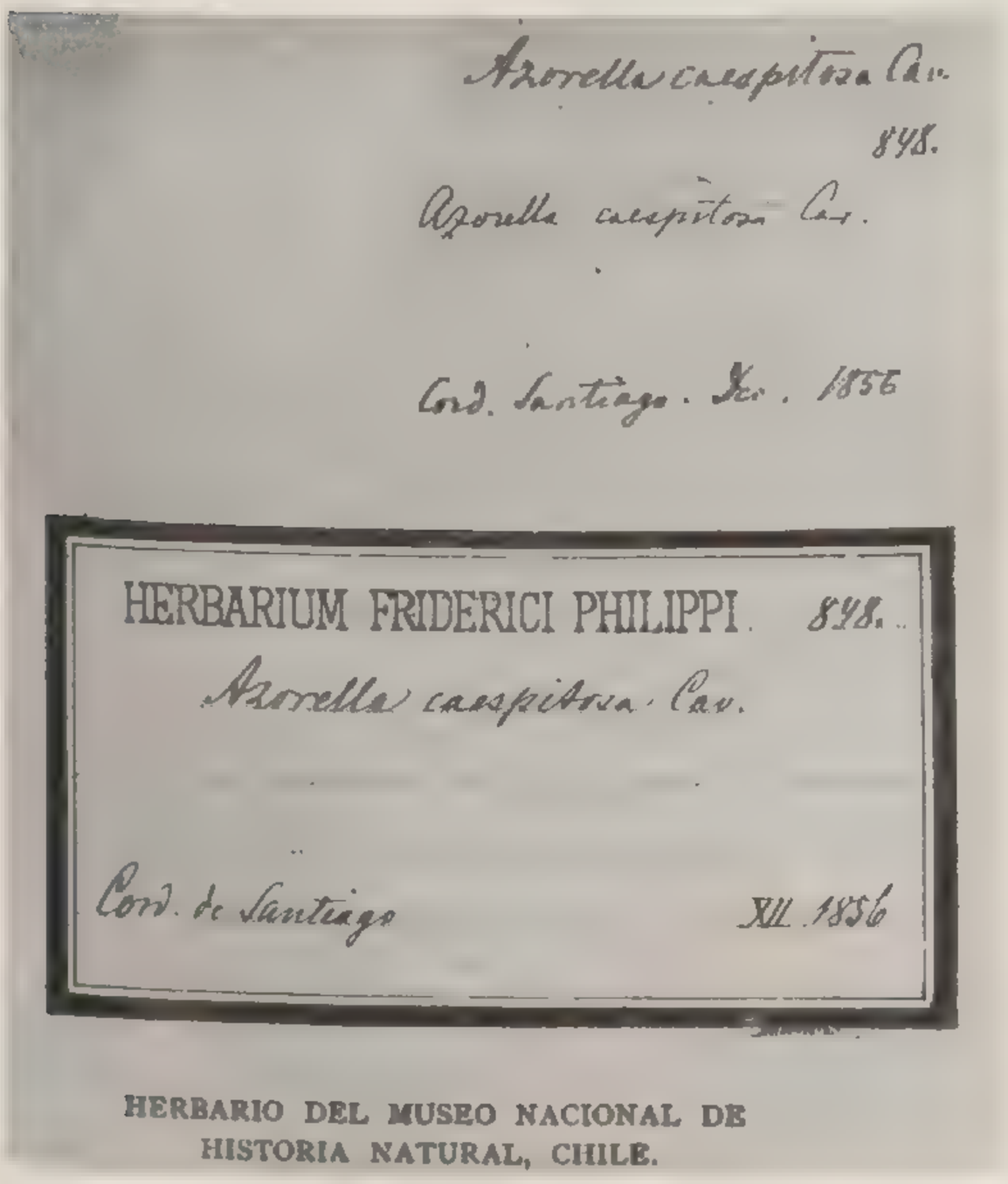

FIGURE 2. Handwriting samples. From top to bottom: annotation by Federico Philippi, label by R. A. Philippi, and label from Federico Philippi's personal collection with his handwriting.

original species description. The known syntypes in the SGO collection have been cataloged along with publication references, collection locality(ies), and SGO accession numbers by Muñoz-Pizarro (1960), with additions by Muñoz-Schick (1973). Neither of these authors attempted to select lectotypes, but concentrated on organizing the material to facilitate work by specialists.

The types of 323 species described by the Philippis remain unlocated (Muñoz-Schick, 1973). However, SGO still houses unmounted, unexamined, mostly duplicate Philippi material in its mounting backlog, and these may yet be discovered. Photographic negatives of both SGO's type material and historical collections of Chilean plants deposited in several European herbaria are available on loan from SGO for study and duplication; the cost of photographic prints, if desired, must be borne by investigators (Muñoz-Pizarro, 1963).

THE PHILIPPIS' PUBLICATIONS

Several bibliographies of works published by the Philippis after their arrival in Chile have been presented, including the collected works (Mostny, 1980) and the principally botanical works (Marticorena, 1992). The number of articles they published was multiplied by their habit, in particular R. A. Philippi's, of publishing the same material more than once. Their purpose was apparently not to enlarge their list of publications, but rather to disseminate their work to a wider audience and also to help struggling journals by providing articles.

We focus here on the Philippis' publications with respect to the flora of Chile, probably a slight majority of the works of R. A. Philippi and certainly most of the publications of Federico. Their publi-

cations can generally be divided into travel accounts, written by one or more frequently both Philippis, and descriptions of new species, written almost exclusively by R. A. Philippi.

R. A. Philippi's descriptions of new species were published principally in several series, although he did not limit himself to these. On a very few occasions he published a new species more than once, in different journals. The first of a series of new species was presented in sections in the German journal *Linnaea* between 1857 and 1865. In these accounts, written in Latin, the new species are grouped by families and numbered consecutively. There is a preface with the first section, and the other sections continue as in one publication. These species are usually based on specimens collected by the Philippis. In some cases a set of consecutive species may be based on specimens from one collecting trip, but this varies also.

Subsequently, R. A. Philippi published more new species in articles in various journals, predominantly Chilean ones. Several of these reported on expeditions by Federico and also other collectors, for whom many species were named. Two notable series of new species were published in the *Anales de la Universidad de Chile*, with descriptions in Latin and Spanish. The first series was published in 1870–1873 and described more than 500 new species. The second, "Plantas nuevas chilenas," was published in 1892–1896. The species in both series were presented following the order used by Gay (1845–1854), which generally follows the system of de Candolle's *Prodromus*. From 1889 on, the descriptions were prepared by both Philippis. The publication of the second series is detailed by Stafleu & Cowan (1983); all of the series are detailed by Marticorena (1992).

It was common during the Philippis' time to issue, in addition to the regular edition of a journal, numerous reprints ("separatas") of individual articles; each had its own pagination, which was often different from the original article. In some cases, the title may also have been changed slightly. These reprints are commonly encountered in libraries, particularly in Chile, as separate articles and in bound volumes of the works of a particular author. We recommend consultation of Muñoz-Pizarro (1960) and Marticorena (1992) as an aid to determining the original publication date, site, and pagination of these articles.

Common nomenclatural problems seen in treatments of Philippi names are the inadvertent creation of *nomina nuda* by later authors, who adopted names that were distributed on specimens but were not published; incorrect citation of publication page number, based on the reprint rather than the original publication; and the incorrect citation of names attributed to R. A. Philippi but effectively published by later authors, most commonly Reiche.

Literature Cited

Barros-Arana, D. 1904. El Doctor Rodulfo Amando Philippi. Su Vida i Sus Obras. Imprenta Cervantes, Santiago, Chile.

Gay, C. 1845–1854. Historia Física y Política de Chile. Botánica [Flora chilena]. Paris, 8 vols., 1 atlas.

Gotschlich, B. 1904. Biografía del Dr. Rodulfo Amando Philippi (1808–1904). Imprenta Central J. Lampert, Valdivia.

———. 1910. Vida i obras de Don Federico Philippi. Bol. Mus. Nac. Hist. Nat. 1(1): 39–80.

Gunckel, H. 1939. La labor botánica de Don Federico Philippi. Revista Univ. (Santiago) 24(1): 13–36.

Marticorena, C. 1992. Bibliografía Taxonómica de las Plantas Vasculares de Chile. Monogr. Syst. Bot. Missouri Bot. Gard. 41.

Mostny, G. (editor). 1980. Biobibliografía, Museo Nacional de Historia Natural 1830–1980. Ministerio de Educación Pública, Dirección de Bibliotecas, Archivos y Museos, Museo Nacional de Historia Natural, Santiago, Chile.

Muñoz-Pizarro, C. 1960. Las Especies de Plantas Descritas por R. A. Philippi en el Siglo XIX. Ediciones de la Universidad de Chile, Santiago.

———. 1963. Fototipos, una valiosa documentación científica en el estudio de las plantas. Publ. Ocas. Mus. Nac. Hist. Nat. 4: 1–18.

Muñoz-Schick, M. 1973. Complemento de "Las Especies de Plantas Descritas por R. A. Philippi en el Siglo XIX." Anal. Univ. Chile, ser. 3, 128: 5–69.

———. 1991. 100 años de la Sección Botánica del Museo Nacional de Historia Natural (1889–1989). Bol. Mus. Nac. Hist. Nat. Chile 42: 181–202.

——— & A. O. Prina. 1987. Nota aclaratoria sobre especies colectadas por Federico Philippi en su viaje a Tarapacá. Noticiario Mensual Mus. Nac. Hist. Nat. Chile 313: 2–17.

Philippi, F. 1881. Catalogus plantarum vascularium chilensium adhuc descriptarum. Anal. Univ. Chile 59: i–viii, 49–422. [Also published separately, viii, 378 pp.]

Stafleu, F. A. & R. S. Cowan. 1983. Taxonomic Literature, Vol. IV: P-Sak. W. Junk, The Hague.

UNA EVALUACION DEL CONOCIMIENTO FLORISTICO DE MEXICO[1]

Victoria Sosa[2] *y Patricia Dávila*[3]

Resumen

En este trabajo se evalúa el conocimiento florístico de México con base en información de colecciones botánicas, herbarios, y estudios florísticos. Las estadísticas indican que con sus casi 2.3 millones de colecciones y sus 71 herbarios, el país alcanza un índice de colección de 117. Dieciséis floras regionales concluídas o en desarrollo abarcan 70% de la superficie del país. Especies estudiadas por estas floras, listados florísticos y principales monografías corresponden al 55% del total de las reportadas para México. Se detectaron como áreas prioritarias de exploración botánica: (1) los bosques de coníferas y encinos, y los bosques tropicales deciduos de la Vertiente del Pacífico; (2) la Sierra Madre del Sur y la Depresión del Balsas; (3) áreas del Norte con vegetación de matorrales xerófilos y pastizales. Grupos con una alta diversidad en el país, como Rubiaceae, requieren aún estudios taxonómicos.

Abstract

This paper evaluates the current floristic knowledge of Mexico based on numbers of botanical collections, herbaria, and floristic studies. Statistics reveal that the country has reached a collection index of 117, with approximately 2.3 million collections and 71 herbaria. Sixteen floras (3 concluded and 13 in process) cover 70% of the national territory. Species included in floristic studies represent 55% of the total reported for Mexico. Active programs of botanical collection are suggested in: (1) conifer-oak forests and deciduous tropical forests of the Pacific slopes; (2) the "Sierra Madre del Sur" and "Depresión del Balsas"; (3) areas of the North, where dry scrubby vegetation is present. Taxonomic studies of some of the most diverse groups distributed in the country, such as Rubiaceae, are still required.

México es un país con una alta riqueza florística. Esta se debe a su extensa superficie territorial, a su diversidad geográfica, y a su ubicación, ya que se encuentra entre el reino biogeográfico Neártico y el Neotropical (Rzedowski, 1978). El número de especies fanerogámicas para México se ha estimado en alrededor de 25,000 (Rzedowski, 1993). La mayoría de éstas se concentran en estados del sur, tales como Chiapas, Oaxaca, y Veracruz. Los tipos de vegetación con una mayor riqueza florística son los bosques de coníferas y de encino (ca. 24% del número total de especies), le siguen los matorrales xerófilos y pastizales (20% del número total de especies), y luego los bosques tropicales subcaducifolios, caducifolios, y espinosos (20% del número total de especies) (Rzedowski, 1993). Rzedowski (1991) estimó que aproximadamente el 10% de los géneros y el 52% de las especies fanerógamicas de México son endémicos, apuntando que el endemismo es más pronunciado en matorrales xerófilos y en pastizales.

El mayor número de especies de plantas en México, como en casi todas las floras mundiales, corresponde a las angiospermas. Las especies de pteridofitas sólo representan el 5% del total de la flora vascular con 1100 especies, de las cuales casi 20% son endémicas (Riba, 1993). Las gimnospermas con aproximadamente 160 especies, constituyen el grupo menos diverso; de éstas casi el 30% corresponden al género *Pinus* (Styles, 1993). Entre las angiospermas, las familias más diversas son: Compositae (2026 especies; Turner & Nesom, 1993), Leguminosae (1724 especies; Sousa & Delgado, 1993), Orchidaceae (1200 especies; Hág-

[1] Agradecemos a J. Rzedowski y L. Cabrera su revisión crítica al manuscrito; a T. Mejía del Consejo Nacional de la Flora de México la información proporcionada; a G. Medina su colaboración en el manejo de información y a M. Escamilla en las ilustraciones; al Consejo Nacional de Ciencia y Tecnología su apoyo económico (0063-N9106 a V. Sosa).

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TABLA 1. Número de colecciones y herbarios en México (con base en *Index Herbariorum*: Holmgren & Keuken, 1974, Holmgren et al., 1981, 1990; Consejo Nacional de la Flora de México, inf. inédita, 1993).

	1974	1981	1990	1993
Colecciones	566,780	1,021,713	2,107,543	2,284,693
Herbarios	18	30	41 (70)	71

sater & Salazar, 1991), Gramineae (1226 especies; Beetle, 1987a), Cactaceae (821 especies; Bravo-Hollis, 1978; Bravo-Hollis & Sánchez-Mejorada, 1991a, b), y Rubiaceae (510 especies; Rzedowski, 1993).

El objetivo del presente trabajo es evaluar el estado actual del conocimiento florístico de México, con base en un análisis del número de: (1) colecciones botánicas; (2) herbarios; y (3) estudios florísticos concluídos o en desarrollo en el país. Basándonos en esta información se plantean perspectivas de los estudios florísticos en México.

COLECCIONES BOTANICAS

El total de colecciones botánicas en México asciende a casi 2.3 millones de ejemplares. Su incremento ha sido notable en las últimas décadas; en 1981 casi se duplicaron con respecto a las colecciones registradas para 1974, y volvieron a duplicarse para 1993 (Tabla 1). El número de colecciones depositadas en herbarios extranjeros es también alto y casi iguala al de los herbarios mexicanos. La cifra estimada por Rzedowski (1976) asciende a alrededor de 1,800,000 de ejemplares, los cuales están albergados en herbarios europeos (B, BM, BR, C, FI, G, HAL, K, LE, M, MA, P, W) y norteamericanos (A, AMES, ARIZ, BH, CAS, F, GH, MO, MICH, MSC, NY, PH, RSA, TEX, VT, UC, WIS, US).

TABLA 2. Algunos ejemplos de índices de densidad de colección en México. (El número de ejemplares fue obtenido a partir de la información proporcionada por los responsables de las Floras de las distintas regiones.)

Estado	Superficie km²	Colecciones	Indice de colección
Baja California Norte	70,113	21,000	29
Durango	119,648	12,600	10
Jaliseo	80,137	197,350	246
México	21,461	181,286	844
Nayarit	27,500	20,000	72
Oaxaca	95,354	50,000	52
Tehuacán-Cuicatlán	10,000	6,000	200
Veracruz	72,815	250,000	343
Yucatán	23,379	37,380	159

Una medida que se ha adoptado para determinar el conocimiento florístico de una zona es un índice de densidad de colección. Este resulta de la relación del número de ejemplares depositados en los herbarios del área dividido entre su superficie (Prance, 1977, 1978). Campbell (1989) ha sugerido un índice de 100 como un mínimo adecuado del conocimiento florístico. México alcanza un índice de 117, el cual sobrepasa este mínimo. Sin embargo, esto no significa que todo el país se encuentre bien explorado botánicamente. Por ejemplo, el estado de Veracruz tiene un índice de densidad de colección de los más altos en el país, de más de 300, mientras que Oaxaca, otro estado con una gran riqueza florística, y Nayarit no alcanzan un índice de 100 (Tabla 2). En el norte del país donde existe un menor número de herbarios y de proyectos florísticos, los índices de densidad de colección aparentemente son bajos. A pesar de que por ejemplo Durango o Baja California posean un índice bajo, presentan grandes áreas ocupadas con el mismo tipo de vegetación, de matorral xerófilo, con una composición florística similar. En estos casos un índice de colección pobre no significa necesariamente que la representación florística no sea adecuada. Asimismo los índices de colección en algunos casos se incrementan cuando se consideran colecciones depositadas en herbarios del extranjero. Por ejemplo, el herbario de la Universidad de California en Berkeley (UC) alberga una buena colección de la Península de Baja California. Del mismo modo, el herbario de la Universidad de Texas en Austin (TEX) contiene una buena representación de colecciones del Desierto Chihuahuense (Rzedowski, 1976).

HERBARIOS MEXICANOS

En la actualidad, el número de herbarios en México asciende a 71. Su incremento ha seguido la misma tendencia que las colecciones, duplicándose en 1981 en comparación con 1974, y en 1993 en comparación con 1981 (Tabla 1). La mayoría de éstos se concentra en el centro del país (Tabla 3), donde se localizan los dos herbarios más grandes, el Herbario Nacional (MEXU) y el herbario del Instituto Politécnico (ENCB); las colecciones de estos dos herbarios suman más de un millón.

TABLA 3. Herbarios de México, con base en el *Index Herbariorum* de Holmgren et al. (1990); los herbarios no registrados en esta obra están marcados con un asterisco*. La información del número de sus colectas se basó en la del Consejo Nacional de la Flora de México, 1993, y su relación aparece en el Apéndice I (sus acrónimos serán determinados posteriormente). Los marcados con doble asterisco** han sido registrados después de la edición de *Index Herbariorum* de 1990 y el número de sus colecciones se basa en información del Consejo de la Flora de México.

Región Norte		Región Oeste		Región Centro		Región Sur	
Baja California Norte		Nayarit		Morelos		Veracruz	
BCMEX	15,000	Univ. Nayarit*	2000	Micológico*	8000	CIB	5000
CMMEX	6000	Aguascalientes		HUMO	5230	Córdoba*	4000
Baja California Sur		CIAN	7000	IMSSM	5500	XAL	200,000
HCIB**	20,000	HUAA	7243	Tlaxcala		XALU	30,000
Sonora		INEGI	11,364	Univ. Tlaxcala*	2000	Oaxaca	
Cent. Pec.*	2000	Jalisco		Hidalgo		OAC	10,000
Chihuahua		CREG	13,000	Univ. Hidalgo*	2000	Tabasco	
Zootecnia*	1500	Normal Jalisco*	3400	Querétaro		CSAT	17,000
Com. Tec.*	3000	GUADA	40,000	Univ. Querétaro*	2000	UJAT	5327
RELC	7000	IBUG	130,000	Puebla		Chiapas	
Coahuila		Agric. Jalisco*	5450	Univ. Puebla*	10,000	CHIP	3780
Laguna*	8100	Ciencias Jalisco*	2500	México		Inv. Sureste*	2000
ANSM	40,000	ZEA**	4000	CHAP	16,611	Yucatán	
Durango		San Luis Potosí		CHAPA	85,000	CICY	6000
CIIDIR	12,600	Zonas Aridas*	2500	CODAGEM	30,000	Univ. Yucatán*	5500
Nuevo León		SLPM	21,372	Cuautitlán*	5000	YUC (EN CICY)	26,380
Linares*	1000	Michoacán		IZTA	14,206	Quintana Roo	
MEMO	2700	EBUM	6500	Univ. Chapingo*	8000	CIQR**	15,000
UNL	54,000	IEB	48,000	XOLO	14,675		
Tamaulipas		CIMI**	5000	Zoot. Chapingo*	5000		
ITCV	9000	Guerrero		Distrito Federal			
UAT	7200	Univ. Guerrero*	3000	AMO	10,000		
Sinaloa				COCA	22,000		
Univ. Sinaloa*	6000			ENCB	503,000		
				FCME	44,055		
				INIA*	17,000		
				INIF	52,000		
				MEXU	550,000		
				UAMIZ	25,000		
				Univ. Xochimilco*	8000		
				Zaragoza*	3000		

TABLA 4. Floras regionales concluídas y en desarrollo en México.

Flora	Número total de especies	Especies incluídas en tratamientos taxonómicos	Referencia
Baja California	2705	2705	Wiggins, 1980
Desierto Sonorense	2634	2634	Wiggins, 1964
Sinaloa	5000	—	Vega, 1990
Durango	4300	—	González et al., 1990
Nayarit	4500	—	Téllez & Flores, 1990
Novogaliciana	?	3523	McVaugh, 1983, 1984, 1985, 1987, 1989, 1992
Bajío y regiones adyacentes	5000	77	Rzedowski & Rzedowski (editores) 1991–1993
Valle de México	2071	2071	Rzedowski & Rzedowski, 1979, 1985, 1989, 1990
Veracruz	7690	1059	Gómez-Pompa (editor), 1978–1991 Sosa (editor), 1992–1993
Tehuacán-Cuicatlán	3000	—	Dávila et al., 1993
Guerrero	6500	15	Diego, 1990 López-Ferrari, 1989
Oaxaca	10,000	—	Dávila et al., 1993
Chiapas	8000	506	Breedlove, 1981 Smith, 1981
Etnoflora Yucatanense	1936	15	Flores et al., 1992 Trejo & Ciau-Uitz, 1992
Jalisco	7000	—	Puga, com. pers.
Mesoamericana	?	(3,243)	Davidse et al., 1994

En esta zona se han fundado varios herbarios recientemente, los cuales no fueron registrados en la última edición de *Index Herbariorum* de Holmgren et al. (1990) (Tabla 3). De la región oeste, solamente el herbario del Instituto de Botánica de la Universidad de Guadalajara (IBUG) alberga más de 100,000 ejemplares. La zona sur posee el menor número de herbarios y colecciones, aunque el tercer herbario más grande del país, el del Instituto de Ecología (XAL), se encuentra localizado en esta área. Estados tales como Zacatecas, Colima, Campeche y Guanajuato carecen por completo de herbarios.

ESTUDIOS FLORISTICOS EN MEXICO

En las primeras décadas de este siglo, los principales estudios florísticos para México eran únicamente los de Standley (1920–1926, 1930). Sin embargo, en los últimos años, tres floras regionales han sido concluídas: las del Desierto de Sonora (Wiggins, 1964), Baja California (Wiggins, 1980) y Valle de México (Rzedowski & Rzedowski, 1979, 1985, 1990), y trece floras regionales están en proceso (Tabla 4). Las 16 floras concluídas o en desarrollo cubren el 70% de la superfice de México. El noreste del país no cuenta con floras regionales (Fig. 1). La mayoría de las floras en desarrollo requieren aún del estudio de más del 50% de los taxa distribuidos en sus zonas. Floras como las de Sinaloa, Nayarit, Durango, Jalisco, y Oaxaca aún no han iniciado la publicación de tratamientos florísticos. Algunas de reciente inicio como las de Tehuacán-Cuicatlán y del Bajío y Regiones Adyacentes, cubren zonas importantes por el número de especies endémicas que contienen o por ser poco conocidas florísticamente.

Los principales estudios taxonómicos que incluyen grupos distribuídos en México (Tabla 5), así como los listados florísticos de áreas geográficas o grupos botánicos (Tabla 6) son otra fuente de información florística. Si se toma el cálculo conservador de 25,000 especies fanerogámicas de México, y si se suman las especies incluídas tanto en floras, como monografías y listados, aproximadamente un 55% han sido estudiadas o listadas, eliminando las especies compartidas.

DISCUSION

México ha incrementado notablemente su infraestructura botánica y sus colecciones en comparación con otros países de Latinoamérica, como por ejemplo Costa Rica (Toledo & Sosa, 1993).

FIGURA 1. Floras de México: 1, Baja California; 2, Desierto Sonorense; 3, Sinaloa; 4, Durango; 5, Nayarit; 6, Novogaliciana; 7, Bajío y regiones adyacentes; 8, Valle de México; 9, Veracruz; 10, Tehuacán-Cuicatlán; 11, Guerrero; 12, Oaxaca; 13, Chiapas; 14, Etnoflora Yucatanense; 15, Jalisco; 16, Mesoamericana.

Asimismo, para alcanzar un índice de colección mínimo se ha requerido un tiempo mucho menor que el que Campbell (1989) había estimado. Sin embargo, las estadísticas aquí presentadas indican que: (1) un 30% de la superficie del país no está considerada en algún estudio florístico, principalmente el noreste del territorio nacional; (2) un 45% de las especies estimadas para el país aún no han sido listadas ni estudiadas taxonómicamente; (3) algunas áreas no están suficientemente exploradas botánicamente; y (4) algunos grupos de plantas requieren mayor atención tanto para su recolección como para su estudio taxonómico.

Si se consideran parámetros tales como bajos índices de colección, porcentaje de endemismos, diversidad florística y fragilidad, de acuerdo con la información previamente presentada, los bosques de coníferas y encinos, y las selvas tropicales deciduas, especialmente de la Vertiente del Pacífico, son áreas prioritarias de recolección. Estas zonas están transformándose rápidamente en grandes desarrollos turísticos y contienen una alta diversidad

TABLA 5. Estudios taxonómicos de los grupos más diversos distribuidos en México.

Grupo de plantas	Número de especies	Especies estudiadas	Referencia
Cactaceae	821	821	Bravo-Hollis, 1978; Bravo-Hollis & Sánchez-Mejorada, 1991a, b
Compositae	aprox. 2026	—	Turner & Nesom (en prensa)
Gramineae	1226	538	Beetle, 1983, 1987b, 1991
Malvaceae	372	372	Fryxell, 1988
Orchidaceae	1200	100	Hágsater & Salazar (editores), 1991
Palmae	100	—	Quero (en preparación)
Pteridophyta (Oaxaca)	690	690	Mickel & Beitel, 1988

TABLA 6. Listados florísticos de México.

Area geográfica o grupo de plantas	Número reportado de especies	Referencia
Chiapas	7018	Breedlove, 1986
Cozumel	542	Téllez & Cabrera, 1987
Durango	3800	González et al., 1991
Estación de Biología Chamela	754	Lott, 1985
Estación de Biología Los Tuxtlas	818	Ibarra & Sinaca, 1987
Península de Yucatán	1936	Sosa et al., 1985
Querétaro	2334	Arguëlles et al., 1991
Quintana Roo	1300	Sousa & Cabrera, 1983
Tabasco	2147	Cowan, 1983
Tehuacán-Cuicatlán	2700	Dávila et al., 1993
Angiospermas acuáticas	111	Lot et al., 1986
Monocotiledóneas Parte 1	393	Espejo & López-Ferrari, 1992
Gramíneas de Puebla	427	Dávila et al., 1990
Pteridofitas de Guanajuato, Michoacán, y Guerrero	300	Díaz & Palacios-Ríos, 1992

de especies que no está representada en las colecciones. De este modo, floras como las de Sinaloa, Jalisco, Guerrero, y Oaxaca, que aún están en una etapa de exploración, podrían dar mayor importancia a la recolección en este tipo de vegetación. Algunas áreas habían sido sugeridas previamente como prioritarias para su exploración por su alto número de endemismos y riqueza florística, tales como la Sierra Madre del Sur en Oaxaca y Chiapas, o la Depresión del Balsas (parte de Guerrero, Oaxaca, y Michoacán) (Lorence & García, 1989). Hasta la fecha estas áreas aún no han sido suficientemente exploradas. Zonas del norte del país, i.e., Zacatecas o Nuevo León, con vegetación de matorral xerófilo y con bajos índices de colección, son también importantes de explorarse.

El describir apropiadamente las especies de una zona exige una buena representación geográfica y de la variabilidad de cada una de las especies (Campbell, 1989). Es así que en estados tales como Chiapas y Oaxaca, con una alta diversidad de especies y bajos índices de colecta, se debe hacer énfasis en recolectar selectivamente para incrementar la representación y variabilidad de las especies.

En cuanto a grupos botánicos, si se continúa con la serie de tratamientos taxonómicos sobre Gramineae y Orchidaceae que se han iniciado (Tabla 5), solamente las Leguminosae y Rubiaceae con una alta diversidad en el país no han recibido un adecuado tratamiento taxonómico. La información de monografías de familias y géneros con menor número de especies en México, está dispersa en la literatura; por lo tanto es muy probable que varios otros grupos botánicos también requieran estudios taxonómicos.

Varios autores han sugerido estrategias para acelerar el conocimiento florístico en áreas tropicales (Mori, 1992; Prance & Campbell, 1988; Raven, 1988). Entre éstas se ha mencionado el desarrollar flórulas de áreas poco conocidas florísticamente, o bien que son interesantes, por su gran diversidad y/o alto endemismo, o por ser regiones más o menos conservadas que están en peligro inminente de desaparecer. Estos autores también han hecho énfasis en que la colaboración internacional entre taxónomos vegetales es importante, así como la construcción de bases de datos florísticas y en la necesidad de estudios monográficos en las zonas neotropicales. Tales estrategias deben ser consideradas en el desarrollo de un programa integrado de mejoramiento del conocimiento florístico de México.

La información aquí presentada indica que a pesar de que numerosas floras regionales cubren casi tres cuartas partes del país, el tiempo requerido para completarlas es muy grande. Asimismo el país no cuenta con una flora a nivel nacional. Por ello es que sugerimos que en forma simultánea al programa de colección y al desarrollo de las floras regionales se inicie una base de datos que permita recuperar fácilmente la información florística. Esta permitirá conocer con precisión el número de especies fanerogámicas distribuídas en México. La construcción de esta base sólo se podrá lograr con la colaboración de todos los herbarios del país, así como de los taxónomos interesados en la flora mexicana.

LITERATURA CITADA

ARGUELLES, E., R. FERNANDEZ & S. ZAMUDIO. 1991. Listado preliminar del estado de Querétaro. Pp. 1-

155 *in* J. Rzedowski & G. C. Rzedowski (editores), Flora del Bajío y Regiones Adyacentes. Fasc. Comp. 2. Instituto de Ecología, A. C., Pátzcuaro.

BEETLE, A. A. 1983. Las Gramíneas de México, Vol. 1. Secretaría de Agricultura y Recursos Hidráulicos, México, D. F.

———. 1987a. Noteworthy grasses from Mexico XIII. Phytologia 63: 209–297.

———. 1987b. Las Gramíneas de México, Vol. 2. Secretaría de Agricultura y Recursos Hidráulicos, México, D. F.

———. 1991. Las Gramíneas de México, Vol. 3. Secretaría de Agricultura y Recursos Hidráulicos, México, D. F.

BRAVO-HOLLIS, H. 1978. Las Cactáceas de México, Vol. 1. Univ. Nacional Autónoma de México, México, D. F.

——— & H. SANCHEZ-MEJORADA. 1991a. Las Cactáceas de México, Vol. 2. Univ. Nacional Autónoma de México, México, D. F.

——— & ———. 1991b. Las Cactáceas de México, Vol. 3. Univ. Nacional Autónoma de México, México, D. F.

BREEDLOVE, D. E. 1981. Introduction to the flora of Chiapas, Part 1. California Academy of Sciences, San Francisco.

———. 1986. Listados Florísticos de México IV. Flora de Chiapas. Instituto de Biología, Univ. Nacional Autónoma de México, México, D. F.

CAMPBELL, D. G. 1989. The importance of floristic inventory in the tropics. Pp. 6–30 *in* D. G. Campbell & H. D. Hammond (editors), Floristic Inventory of Tropical Countries. New York Botanical Garden, New York.

COWAN, C. P. 1983. Listados florísticos de México I. Flora de Tabasco. Instituto de Biología, Univ. Nacional Autónoma de México, México, D. F.

DAVIDSE, G., M. SOUSA S. & A. O. CHATER (editores). 1994. Flora Mesoamericana, Vol. 6, Alismataceae a Cyperaceae. Univ. Nacional Autónoma de México, México D. F.; Missouri Botanical Garden, St. Louis; The Natural History Museum, London.

DAVILA, P., P. TENORIO, E. MANRIQUE, A. MIRANDA & A. RODRIGUEZ. 1990. Listados florísticos de México VIII. Listado florístico de las Gramíneas de Puebla. Instituto de Biología, Univ. Nacional Autónoma de México, México, D. F.

DAVILA, P., J. L. VILLASEÑOR, R. MEDINA, A. RAMIREZ, A. SALINEAS, J. SANCHEZ-KEN & P. TENORIO. 1993. Listados Florísticos de México X. Flora del Valle de Tehuacán-Cuicatlán. Instituto de Biología, Univ. Nacional Autónoma de México, México, D. F.

DIAZ, H. & M. PALACIOS-RIOS. 1992. Listado preliminar de especies de pteridofitas de los estados de Guanajuato, Michoacán y Querétaro. Pp. 1–57 *in* J. Rzedowski & G. C. Rzedowski (editores), Flora del Bajío y Regiones Adyacentes. Fasc. Comp. 3. Instituto de Ecología, A. C., Pátzcuaro.

DIEGO, N. 1990. Flora del estado de Guerrero. Pp. 494 *in* Resúmenes del XI Congreso Mexicano de Botánica, Sociedad Botánica de México, México, D. F.

ESPEJO, A. & A. LOPEZ-FERRARI. 1992. Las monocotiledóneas mexicanas: Una sinopsis florística. 1. Lista de Referencia. Vol. 1. Consejo Nacional de la Flora de México-Univ. Metropolitana Iztapalapa, México, D. F.

FLORES, J. S., H. NARAVE & A. P. VOVIDES. 1992. Gymnospermae. *In* J. S. Flores (editor), Etnoflora Yucatanense. Fasc. 5. Univ. Autónoma de Yucatán, Mérida.

FRYXELL, P. A. 1988. Malvaceae of Mexico. Syst. Bot. Monogr. 25: 1–522.

GOMEZ-POMPA, A. (editor). 1978–1991. Flora de Veracruz. Fasc. 1–66. Instituto Nacional de Investigaciones sobre Recursos Bióticos-Instituto de Ecología A. C., Xalapa, Veracruz.

GONZALEZ, S., M. E. GONZALEZ & H. ARRIETA. 1991. Listados florísticos de México IX. Flora de Durango. Instituto de Biología, Univ. Nacional Autónoma de México, México, D. F.

———, ———, ——— & A. GARCIA. 1990. La flora de Durango. Pp. 494 *in* Resúmenes del XI Congreso Mexicano de Botánica, Sociedad Botánica de México. México. D. F.

HAGSATER, E. & G. SALAZAR (editores). 1991. Orquídeas de México. Icones Orchidacearum, Vol. 1. Asociación Mexicana de Orquideología, México, D. F.

HOLMGREN, P. K. & W. KEUKEN. 1974. Index herbariorum, Part 1. The herbaria of the world, ed. 6. Regnum Veg. 92.

———, N. H. HOLMGREN & I. BARNETT. 1990. Index herbariorum, Part 1. The herbaria of the world, ed. 8. Regnum Veg. 120.

———, W. KEUKEN & E. K. SCHOFIELD. 1981. Index herbariorum, Part 1. The herbaria of the world, ed. 7. Regnum Veg.106.

IBARRA, G. & S. SINACA. 1987. Listados florísticos de México VII. Estación de Biología Tropical Los Tuxtlas, Veracruz. Instituto de Biología, Univ. Nacional Autónoma de México, México, D. F.

LOPEZ-FERRARI, A. R. 1989. Araliaceae. Pp. 1–23 *in* N. Diego (editor), Flora de Guerrero, Vol. 1. Facultad de Ciencias, Univ. Nacional Autónoma de México, México, D. F.

LORENCE, D. H. & A. GARCIA. 1989. Oaxaca, Mexico. Pp. 253–269 *in* D. G. Campbell & H. D. Hammond (editors), Floristic Inventory of Tropical Countries. New York Botanical Garden, New York.

LOT, A., A. NOVELO & P. RAMIREZ-MERCADO. 1986. Listados Florísticos de México V. Angiospermas Acuáticas Mexicanas 1. Instituto de Biología de la Univ. Nacional Autónoma de México, México, D. F.

LOTT, E. J. 1985. Listados florísticos de México III. La Estación de Biología Chamela, Jalisco. Instituto de Biología, Univ. Nacional Autónoma de México, México, D. F.

MCVAUGH, R. 1983. Gramineae. *In* W. R. Anderson (editor), Flora Novogaliciana, Vol. 14. Univ. Michigan Press, Ann Arbor.

———. 1984. Compositae. *In* W. R. Anderson (editor), Flora Novogaliciana, Vol. 12. Univ. Michigan Press, Ann Arbor.

———. 1985. Orchidaceae. *In* W. R. Anderson (editor), Flora Novogaliciana, Vol. 16. Univ. Michigan Press, Ann Arbor.

———. 1987. Leguminosae. *In* W. R. Anderson (editor), Flora Novogaliciana, Vol. 5. Univ. Michigan Press, Ann Arbor.

———. 1989. Bromeliaceae to Dioscoreaceae. *In* W. R. Anderson (editor), Flora Novogaliciana, Vol. 15. Univ. Michigan Press, Ann Arbor.

———. 1992. Gymnosperms and Pteridophytes. *In* W. R. Anderson (editor), Flora Novogaliciana, Vol. 17. Univ. Michigan Press, Ann Arbor.

MICKEL, J. T. & J. M. BEITEL. 1988. Pteridophyte Flora of Oaxaca, Mexico. Mem. New York Bot. Gard. 46: 1–568.

MORI, S. 1992. Neotropical floristics and inventory: Who will do the work? Brittonia 44: 372–375.

PRANCE, G. T. 1977. Floristic inventory of the tropics: Where do we stand? Ann. Missouri Bot. Gard. 64: 659–684.

———. 1978. Floristic inventory of the tropics: A correction. Ann. Missouri Bot. Gard. 65: i–ii.

——— & D. G. CAMPBELL. 1988. The present state of tropical floristics. Taxon 37: 519–548.

RAVEN, P. H. 1988. Tropical floristics tomorrow. Taxon 37: 549–560.

RIBA, R. 1993. Mexican Pteridophytes: Distribution and endemisms. Pp. 379–395 *in* T. P. Ramamoorthy, R. Bye, A. Lot. & J. Fa (editors), Biological Diversity of Mexico: Origins and Distribution. Oxford Univ. Press, New York.

RZEDOWSKI, J. 1976. Catálogo de los herbarios institucionales mexicanos. Sociedad Botánica de México, México, D. F.

———. 1978. Vegetación de México. Limusa, México, D. F.

———. 1991. El endemismo en la flora fanerogámica mexicana: Una apreciación analítica preliminar. Acta Botánica Mexicana 15: 47–64.

———. 1993. Diversity and origins of the phanerogamic Flora of Mexico. Pp. 129–148 *in* T. P. Ramamoorthy, R. Bye, A. Lot & J. Fa (editors), Biological Diversity of Mexico: Origins and Distribution. Oxford Univ. Press, New York.

——— & G. C. RZEDOWSKI. 1979. Flora Fanerogámica del Valle de México, Vol. 1. Compañía Editorial Continental, México, D. F.

——— & ———. 1985. Flora Fanerogámica del Valle de México, Vol. 2. Escuela Nacional de Ciencias Biólogicas-Instituto de Ecología, A. C. México, D. F.

——— & ———. 1989. Sinopsis numérica de la flora fanerogámica del Valle de México. Acta Botánica Mexicana. 8: 15–30.

——— & ———. 1990. Flora Fanerogámica del Valle de México, Vol. 3. Instituto de Ecología, Pátzcuaro.

——— & ——— (editores). 1991–1993. Flora del Bajío y Regiones Adyacentes. Fasc. 1–16. Instituto de Ecología, A. C., Pátzcuaro.

SMITH, A. R. 1981. Pteridophytes. *In:* D. E. Breedlove (editor), Flora of Chiapas. Proc. Calif. Acad. Sci. 2: 1–370.

SOSA, V. (editora). 1992–1993. Flora de Veracruz. Fasc. 67–72. Instituto de Ecología, A. C., Xalapa, Veracruz.

———, J. S. FLORES, V. RICO-GRAY, R. LIRA & J. J. ORTIZ. 1985. Lista Florística y Sinonimia Maya. *In:* V. Sosa (editor), Etnoflora Yucatanense, Vol. 1. Instituto Nactional de Investigaciones sobre Recursos Bióticos, Xalapa.

SOUSA, M. & E. F. CABRERA. 1983. Listados florísticos de México II. Flora de Quintana Roo. Instituto de Biología, Univ. Nacional Autónoma de México, México, D. F.

——— & A. S. DELGADO. 1993. Mexican Leguminosae: Phytogeography, endemism, and origins. Pp. 459–511 *in* T. P. Ramamoorthy, R. Bye, A. Lot & J. Fa (editors), Biological Diversity of Mexico: Origins and Distribution. Oxford Univ. Press, New York.

STANDLEY, P. C. 1920–1926. Trees and shrubs of Mexico. Contr. U.S. Natl. Herb. 23: 1–1721.

———. 1930. Flora of Yucatan. Field Mus. Nat. Hist., Bot. Ser. 3: 157–492.

STYLES, B. T. 1993. Genus *Pinus*: A Mexican preview. Pp. 397–420 *in* T. P. Ramamoorthy, R. Bye, A. Lot & J. Fa (editors), Biological Diversity of Mexico: Origins and Distribution. Oxford Univ. Press, New York.

TELLEZ, O. & E. C. CABRERA. 1987. Listados Florísticos de México VI. Flórula de la Isla de Cozumel, Quintana Roo. Instituto de Biología, Univ. Nacional Autónoma de México, México, D. F.

——— & A. FLORES. 1990. La flora de Nayarit. Pp. 494 *in* Resúmenes del XI Congreso Mexicano de Botánica. Sociedad Botánica de México, México, D. F.

TOLEDO, V. M. & V. SOSA. 1993. Floristics in Latin America and the Caribbean: An evaluation of the number of plant collections and botanists. Taxon 42: 355–364.

TREJO, J. C. & R. CIAU-UITZ. 1992. Psilotaceae. *In:* J. S. Flores (editor), Etnoflora Yucatanense, Vol. 6. Univ. Autónoma de Yucatán, Mérida.

TURNER, B. L. & G. L. NESOM. 1993. Biogeography, diversity and endangered or threatened status of Mexican Asteraceae. Pp. 559–576 *in* T. P. Ramamoorthy, R. Bye, A. Lot & J. Fa (editors), Biological Diversity of Mexico: Origins and Distribution. Oxford Univ. Press, New York.

——— & ——— (editors). Asteraceae of Mexico. University of Texas, Austin. (En prensa.)

VEGA, R. 1990. Flora de Sinaloa. P. 366 *in* Resúmenes del XI Congreso Mexicano de Botánica. Sociedad Mexicana de Botánica, México, D. F.

WIGGINS, I. L. 1964. Flora of the Sonoran Desert. *In:* F. Shreve & I. L. Wiggins (editors), Vegetation and Flora of the Sonoran Desert, Vols. 1, 2. Stanford Univ. Press. Stanford, California.

———. 1980. Flora of Baja California. Stanford Univ. Press. Stanford, California.

APENDICE I. Herbarios Mexicanos no registrados en Index Herbariorum.

Agric. Jalisco: Herbario, Facultad de Agricultura de la Universidad de Guadalajara, Km. 14.5 carretera Nogales–Las Agujas, Ejido Nextipac, 45220 Guadalajara, Jalisco.

Cent. Pec.: Herbario Regional del Centro de Investigaciones Pecuarias del Estado de Sonora, SARH, Apdo. Postal 18, 83380 Carbó, Sonora.

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Com. Tec.: Herbario, Brigada II de la Comisión Técnico Consultiva para la Determinación de los Coeficientes de Agostadero, SARH, Medicina 9037 A, Chihuahua, Chihuahua.

Córdoba: Herbario Jerzy Rzedowski, Universidad Veracruzana, Campus Córdoba, Zona Córdoba-Orizaba, Km. 1 camino Peñuela Amatlán *s.n.*, Peñuela, Veracruz.

Cuautitlán: Herbario, Facultad de Estudios Superiores de Cuautitlán, Universidad Nacional Autónoma de Mé-

xico, Departamento de Ciencias Biológicas, Km. 3 carretera Cuautitlán–Teoloyucan, Estado de México.

Inv. Sureste: Herbario del Centro de Investigaciones Ecológicas del Sureste, Apdo. Postal 63, 29200 San Cristóbal de las Casas, Chiapas.

Laguna: Herbario, Universidad Autónoma Agraria "Antonio Narro," Unidad Laguna, carretera a Santa Fe y Periférico, Apdo. Postal 940. 27000 Torreón, Coahuila.

Linares: Herbario, Facultad de Silvicultura y Manejo de Recursos Renovables, Universidad Autónoma de Nuevo León, Unidad Linares, Apdo. Postal 41, 67700 Linares, Nuevo León.

Micológico: Herbario Micológico de Morelos, Universidad Autónoma del Estado de Morelos, Facultad de Ciencias Biológicas, Av. Universidad 10001, Col. Chamilpa, 62210 Cuernavaca, Morelos.

Normal Jalisco: Herbario, Escuela Normal Superior de Jalisco, Calle Alejandro No. 3317, Vallarta San Jorge, Guadalajara, Jalisco.

Univ. Chapingo: Herbario, Hortorio "Prof. Jorge Espinosa Salas," Universidad Autónoma de Chapingo, Km. 38.5 carretera México–Texcoco, 56230 Chapingo, México.

Univ. Guerrero: Herbario, Escuela Superior de Agricultura, Universidad Autónoma de Guerrero, Periférico Poniente *s.n.*, Iguala, Guerrero.

Univ. Hidalgo: Herbario Regional, Universidad Autónoma de Hidalgo, Centro de Investigaciones Biológicas, carretera Pachuca–Tulancingo *s.n.*, 42000 Pachuca, Hidalgo.

Univ. Nayarit: Herbario, Coordinación de la Investigación Cientifica, Universidad Autónoma de Nayarit, Domicilio Conocido, Tepic, Nayarit.

Univ. Puebla: Herbario, Facultad de Ciencias, Universidad Autónoma de Puebla, 4 Sur 104, Puebla, Puebla.

Univ. Querétaro: Herbario, Universidad Autónoma de Querétaro, Apdo. Postal 494, 76010 Querétaro, Querétaro.

Univ. Sinaloa: Herbario, Escuela Superior de Agricultura "González Ortega," Universidad Autónoma de Sinaloa, Apdo. Postal 726, 80000 Culiacán, Sinaloa.

Univ. Tlaxcala: Herbario, Universidad Autónoma de Tlaxcala, Centro de Investigaciones Biológicas, Apdo Postal 12, Ixtacuixtla, Tlaxcala.

Univ. Xochimilco: Herbario, Unidad de servicio y apoyo al diagnóstico del Departamento de Producción Agrícola y Animal, Universidad Autónoma Metropolitana-Xochimilco, Calzada del Hueso 1100, Col. Villa Quietud, 04960 México, D.F.

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PALEOBIOGEOGRAPHIC DISTRIBUTION OF *KUYLISPORITES* AND ITS POSSIBLE RELATIONSHIP TO THE EXTANT FERN GENUS *CNEMIDARIA* (CYATHEACEAE)[1]

Barbara A. R. Mohr[2] *and David B. Lazarus*[2]

Abstract

The fossil spore genus *Kuylisporites* contains four species, of which *K. mirabilis*, *K. separatus*, and *K. scutatus* seem to be restricted to the Cretaceous and Paleogene of the Northern Hemisphere. The fourth species, *K. waterbolkii*, a spore that has identical features with the spore of the extant fern genus *Cnemidaria*, has been found exclusively in Tertiary to Holocene sediments of the Southern Hemisphere, with a trend to increasing restriction to the Neotropics. *Kuylisporites waterbolkii* has been found in the southern Gondwanan realm from the Early Eocene through early Miocene. New occurrences of *K. waterbolkii*, in middle Eocene sediments from the South Orkney area (Antarctica), link the Paleogene Australian and South American distribution. Between the late Eocene and Oligocene, when dramatic glacial cooling took place, *K. waterbolkii* migrated north. In Australia, where climatic deterioration was balanced by northward drift, *K. waterbolkii* persisted until the early Miocene. Increasing drought in Australia during the Neogene led, however, to its extinction. In South America the distribution area shifted from high latitudes during the Eocene, when climatic conditions there were warm to temperate, to low latitudes during the Oligocene. From the Oligocene on *K. waterbolkii* has been found exclusively in an area that overlaps with the area of extant *Cnemidaria*, which lives mostly in (sub)montane forests in tropical Central/South America and the Antilles. Morphological identity and overlapping paleobiogeographic distribution from the Miocene on suggest that *K. waterbolkii* can be correlated with spores of extant *Cnemidaria*. If this is the case, the Recent area of distribution of *Cnemidaria* must be considered to be a relict area.

Broad austral biogeographic distributions of a large number of plant taxa have been known since work by early botanists such as Hooker in the 1840s (Hooker, 1847). Hooker noticed, for example, that the Falkland Islands, South Georgia, Tristan da Cunha (all in the South Atlantic), and the Kerguelen Islands in the South Indian Ocean, as well as islands south of New Zealand, about 8000 km away from South America, contain plants closely related to taxa from Tierra del Fuego. These observations led botanists, such as, e.g., Engler (1882), to conclude that Antarctica might have had a bridge function, connecting South America and Australia; these hypotheses were proposed well before modern plate tectonics had explained the fragmentation of Gondwana and subsequent continental movements (Wegener, 1926).

Some plants, including fern, conifer, and angiosperm taxa, are currently distributed on only one of the Southern Hemisphere continents, whereas the paleobotanical record shows a more widespread distribution. Examples of this pattern are the co-

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nifer *Microcachrys* Hook., today restricted to Tasmania but, according to the pollen record, widely distributed in Cretaceous and Tertiary times throughout Gondwana, including Antarctica (Cookson & Pike, 1954).

Antarctica was considered by Copeland (1930) as the possible center of development of many fern families and, in addition, as a bridge between the Gondwanan continents. Even though the idea of Antarctica as an origination center for many ferns is nowadays widely abandoned, the bridge function of this southern continent had been confirmed for certain fern taxa by contemporary palynologists. Askin (1989) was able to show by means of heterochronous stratigraphic occurrences that the Antarctic Peninsula acted as a dispersal corridor in both directions between South America and Australasia for two fern morphs: *Clavifera triplex* Bolkhovitina, a gleicheniaceous fern, and *Azolla* spp., a ubiquitous water fern.

Cyatheacidites annulatus Cookson ex Potonié is another example of fern migration based on fossil spore data. This fern spore can be correlated with the extant fern genus *Lophosoria* (Dettmann, 1986). *Lophosoria* occurs today throughout much of South and Central America and the Greater Antilles in wet (montane) temperate environments at high altitudes, mostly over 2000 m. Only in southern South America does it also grow at low altitudes. In past geologic times, however, this genus is not known from the tropics, but instead it is known to have occurred in southern high latitudes—in southern South America from the early Cretaceous to the Oligocene, in Antarctica from the early Cretaceous to the middle Eocene, and in Australia and New Zealand until the Pliocene (Dettmann, 1986).

New evidence from *Kuylisporites waterbolkii* Potonié (1956)—a spore identical in appearance to the spores of the extant fern genus *Cnemidaria* Presl (Cyatheaceae)—from sediments of the South Orkney region (Antarctica) adds further credence to the idea that fern taxa have at least occasionally migrated from original high-latitude Southern Hemisphere distributions into lower latitude regions in the Cenozoic.

The high number of *Cnemidaria* species (23 according to Stolze, 1974; plus 2 by Moran, 1990) in northern South America (Colombia and Venezuela), as well as the occurrence there of the most primitive species, led Stolze (1974) to the conclusion that the genus may have originated in this area and migrated to more northerly and southerly sites (Central America and central South America). According to the fossil spore evidence, however, the genus might have had a more widespread distribution during the Paleogene in the Southern Hemisphere.

The occurrence of *Cnemidaria*-type spores during the early to mid-Middle Eocene in Antarctica can be used as a valuable tool in reconstructing paleobiogeographic distribution patterns and paleoclimatic and environmental conditions during the Cenozoic climatic optimum in southern high latitudes (about 60°S). This climax of Cenozoic warmth is known to have occurred during the time interval of about 58 to 45 Ma. and has been documented in the Weddell Sea and southern Indian Ocean regions by microfossil groups such as foraminifera (Stott & Kennett, 1990; Thomas, 1990) and dinoflagellates (Mao & Mohr, in press; Mohr & Mao, in prep.), and by stable isotope data (Hsü et al., 1984; Kennett & Barker, 1990; Barrera & Huber, 1991).

The Fossil Spores

The genus *Kuylisporites* contains four species: *K. mirabilis* (Bolkhovitina) Krutzsch, *K. separatus* Chlonova, *K. scutatus* Newman, and *K. waterbolkii*. Excluded from our considerations are the species with a completely different wall structure, which suggest a non-cyatheacean origin. Not considered is, for example, *Kuylisporites lunaris* Cookson & Dettmann, 1958, because it lacks the typical thickenings in the equatorial region and the three well-defined pores, located at the center of the three sides. Dettmann (1963) already stated that *K. lunaris*, found in the Upper Mesozoic of southeastern Australia, differs from all the other known species of *Kuylisporites*.

The oldest species of *Kuylisporites* clearly belonging to the Cyatheaceae is *K. mirabilis*, known from the Cenomanian of Siberia (Bolchovitina, 1953). It also has been reported from the Senonian of the Netherlands and from the Paleogene of Germany (Krutzsch, 1959), where it might have been reworked from Cretaceous sediments (Krutzsch, pers. comm.). Chlonova (1960) found in the Maastrichtian and Paleogene of western Sibiria a medium-sized (30–34 μm, average size 32 μm) species of *Kuylisporites*, *K. separatus*, with small rugae on the surface. In this respect, the spore is similar to the North American species *K. scutatus*.

In North America *K. scutatus* existed during the Campanian to Paleocene. It is reported from Colorado (Newman, 1964, 1965), Texas (Evitt, 1973; Beeson, 1992), and New Jersey (Traverse, pers. comm.). This species is very small (average size 27 μm) compared with the (younger) Southern

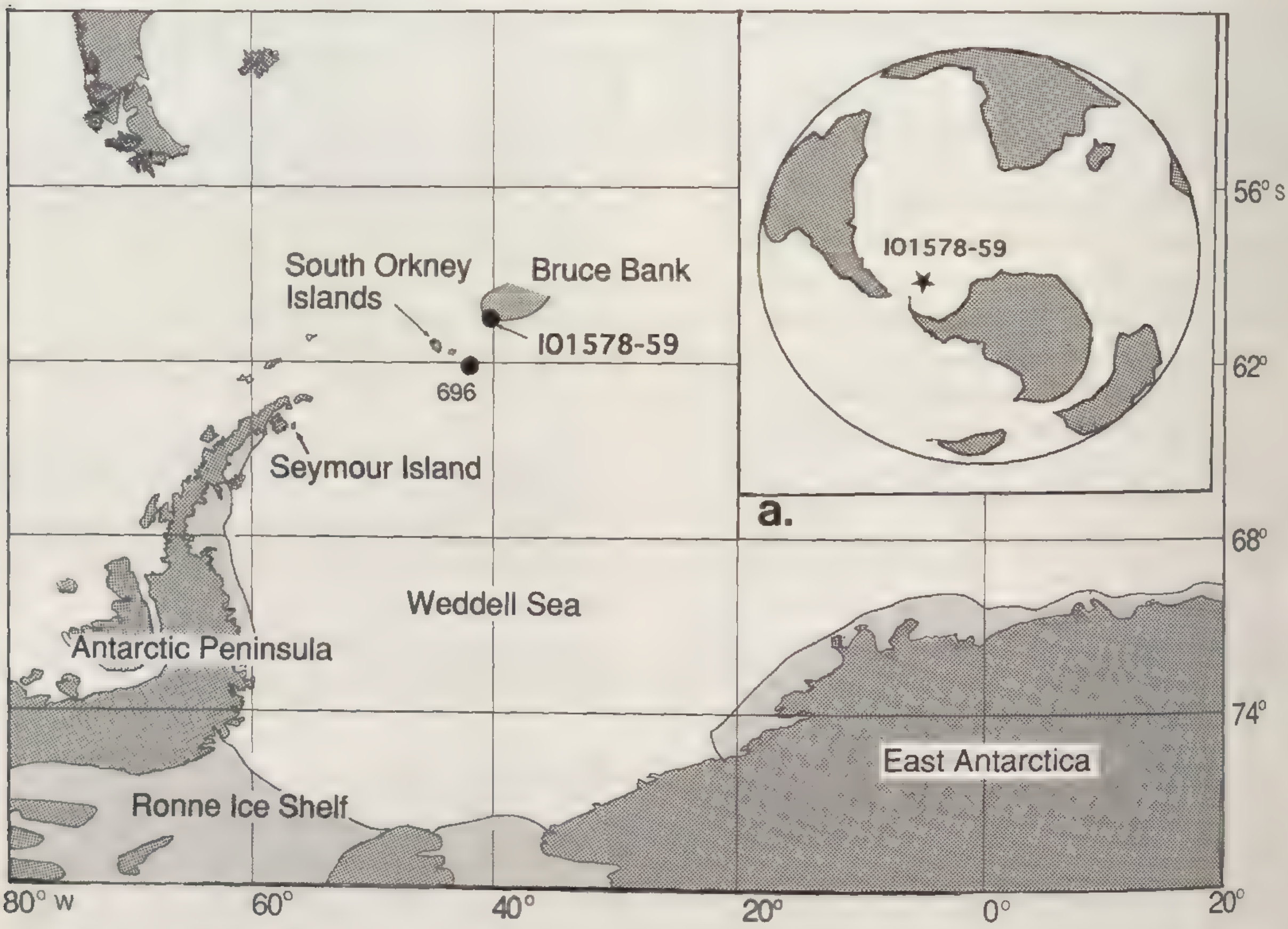


FIGURE 1. Location map of Weddell Sea, Antarctica showing location of Florida State piston core Islas Orcadas (IO) 1578-59, Ocean Drilling Program Site 696, and other geographic features referred to in the text. Light stipple pattern along edge of Antarctic continent indicates ice-shelf. Inset (a) shows approximate location of core IO1578-59 in middle Eocene times. Continental reconstruction created using Terra Mobilis program of Denham & Scotese (1987).

Hemisphere species *K. waterbolkii* and has, according to the original description, a slightly rugulate surface on the distal side (Newman, 1965). Furthermore, this species lacks any additional scattered pores.

Kuylisporites waterbolkii is known from the late Early Eocene on from southeastern Australia (Stover & Partridge, 1973). *Kuylisporites waterbolkii*, often named *Hemitelia* by various authors (see below), has been observed in Central and South America from the Oligocene on.

A list of the known fossil occurrences of the spore genus *Kuylisporites* is given in an Appendix to this paper.

SPORES FROM BRUCE BANK, OFF THE NORTHERN ANTARCTIC PENINSULA

a. Material and method

New evidence has been found from middle Eocene (43–50 Ma.) marine strata from the South Orkney area (Fig. 1). The material was collected during the Islas Orcadas cruise 1578 (Cassidy, 1980), at Bruce Bank, South Scotia Ridge off the northern Antarctic Peninsula (Latitude 60°33′S; Longitude 40°13′W; mbsl: 2707 m, see Fig. 1). According to Toker et al. (1991), the nannofossil assemblage found in these strata can be assigned to the *Chiasmolithus gigas* Subzone of the *Nannotetrina quadrata* Zone, which equals late early to mid Middle Eocene. Following Berggren et al.'s (1985) timescale, an absolute age of about 47 to 49 Ma. (see Bolli et al., 1985) can be estimated.

The material for this study comes from the upper 130 cm of a 3.85-m-long piston core (IO1578-59), which contains olive gray to olive brown compacted clay. From this interval six samples were taken, which were processed using standard centrifuge preparation techniques. In addition, sieving with a 15 μm sieve and oxidation with HNO_3 were also carried out. The latter procedure was necessary because of the high amount of pyrite that filled a good part of the palynomorphs. From every sample four smear slides mounted with glycerine jelly were prepared.

The material is rich in well-preserved dinofla-

gellate cysts (Mao & Mohr, in press), fungal and fern spores, and gymnosperm and angiosperm pollen (Mohr, in prep.).

From Core IO1578-59 more than 30 different spore taxa were identified, with an average diversity of about 15 to 20 taxa per sample (Mohr, in prep.). Most of these spore taxa can be assigned to ferns; a few genera, however, have been derived from mosses and lycopods. *Cnemidaria*-type spores occur regularly, but with a frequency of only about 2 to 4 specimens per slide, equaling about 0.5% to 1.0% of the total sporomorph content.

b. Description of Cnemidaria*-type spores from the South Orkney area*

Kuylisporites waterbolkii Potonié (1956), Figure 2A, B, C.

Trilete spores, amb rounded triangular. Laesurae unthickened, straight, long (up to ⅘ of the total spore diameter). Foveolate, small fovae (1–5 μm) scattered irregularly over the entire spore surface. Three large pits (diameter about 5–7 μm) are found symmetrically arranged at the center of the three sides. There, the thickness of the two-layered wall is usually increased (from 1.5 to 3 μm). Size of the spores: 27–(32)–35 μm.

Comments: In size somewhat smaller than spores of most extant species of *Cnemidaria*, but otherwise identical.

Geography and Ecology of Extant *Cnemidaria*

The geographic range of living *Cnemidaria* with its 25 species (Moran, 1990) covers the area of Central America, the Greater Antilles, and the northern part of South America (Tryon & Tryon, 1982). The distribution is generally continuous, with species overlapping through most of the range (Stolze, 1974). There are however, according to this author, two notable regions of disjunction: southeastern Brazil, and an area containing the Mexican provinces of Chiapas and Oaxaca and the Guatemaltecan province of Alta Verapaz.

Most *Cnemidaria* species have a subarborescent habit, with leaves usually less than 1 m in length. These ferns are largely confined to deeply shaded, moist habitats, in or at the edges of forests, sometimes along creeks and waterfalls, at elevations ranging from sea level to 2300 m, but typically between 500 and 2000 m (Stolze, 1974). Lellinger (1975) reported *Cnemidaria* from Colombia (Depto. del Chocó), where it was mostly seen at roadsides at altitudes at or below 500 m, rarely up to 1000 m. Mägdefrau (1960) gave more precise data for one of the areas of occurrence of *Cnemidaria*, in the cloud forests of the "Rancho Grande" in northern Venezuela. There, the cloud forest is found at altitudes between 1150 m and about 2350 m. The annual precipitation is about 1750 mm, with most of the precipitation (1600 mm) falling during the season from April through November. Daily temperature ranges are generally low (16–21°C).

The Spores of Extant *Cnemidaria*

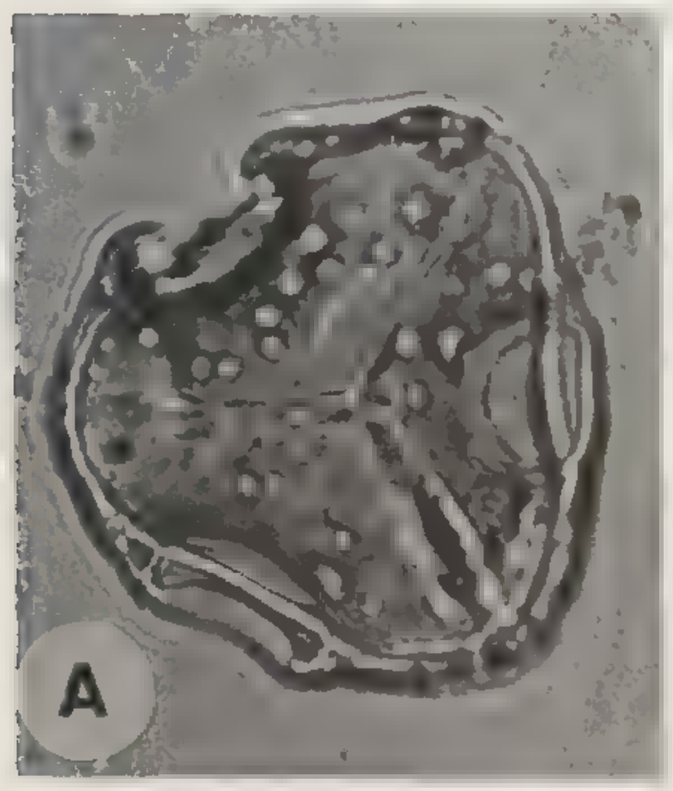
Many features of the extant genus *Cnemidaria* are partially shared with other cyatheacean genera (Stolze, 1974; Tryon & Tryon, 1982), but trilete spores with three large pits are unique to this fern genus. *Cnemidaria* spores are characterized by three pores in the equatorial area, equidistant between the laesurae and often with additional smaller pores (Fig. 2). In fact, this spore type is graphically so special that the Laboratory of Palynology of the University of Amsterdam (Hugo de Vries-Laboratorium) chose the outline of this taxon as its logo.

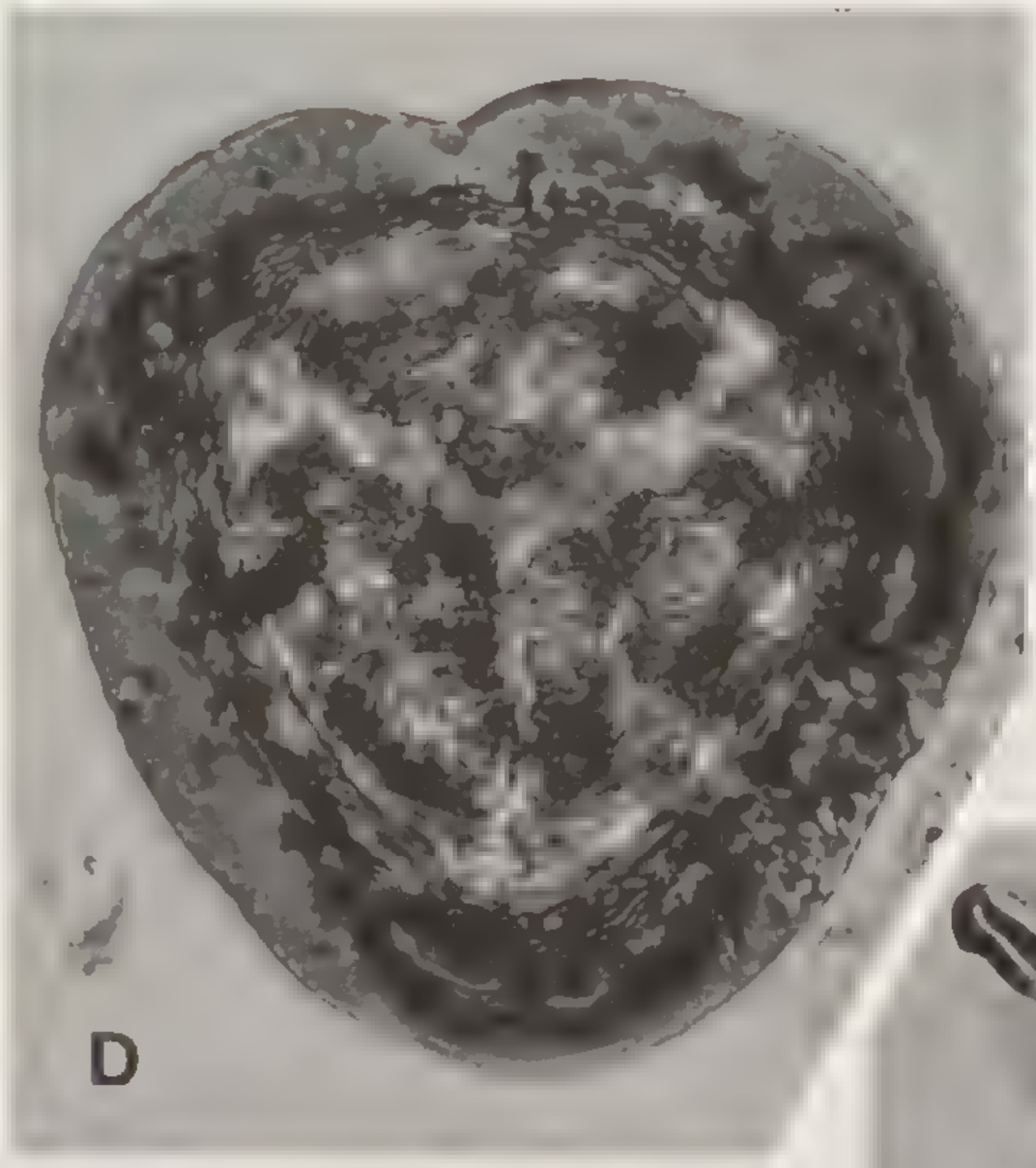
Spores of extant *Cnemidaria* were previously described in detail by Erdtman & Sorsa (1971) and by Stolze (1974), and were well documented by Tryon & Lugardon (1991). According to Stolze (1974) the approximate lateral diameter is 37 to 52 μm. The surface of the exospore is more or less smooth, but shows three typical large pores (up to 15 μm diam.), located at the center of each of the three sides. Additional pores of different size may be distributed randomly over the spore surface.

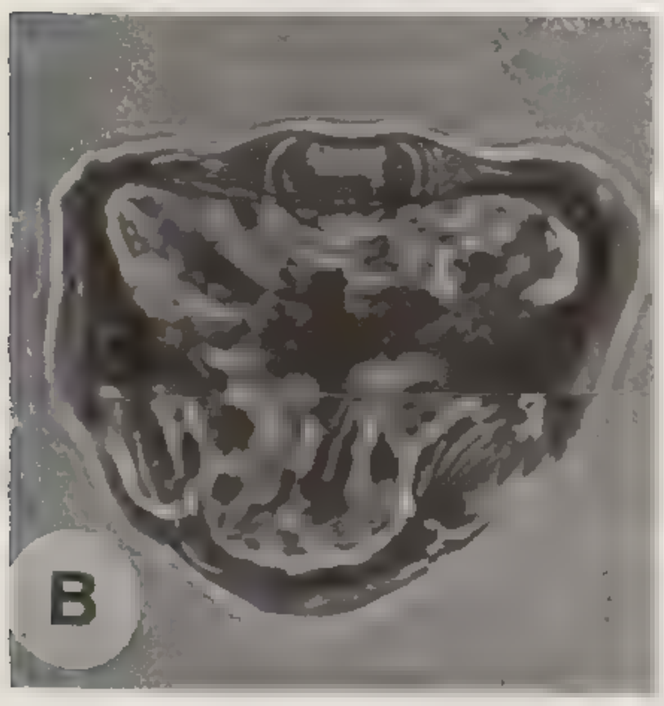
We have examined spores from the following extant species: *C. choricarpa* (Maxon) Tryon, Costa Rica, *Pittier & Durand 4835*; *C. cocleana* Stolze, Panama, *Franco 14880*; *C. horrida* (L.) Presl, Venezuela, *A. Smith 948*; *C. mutica* (Christ) Tryon, Costa Rica, *Hennipman 6739*; *C. roraimensis* (Domin) Tryon, Guyana, *Pipoly 10789*; *C. spectabilis* (Kunze) Tryon, French Guyana, *Cremers 10172*.

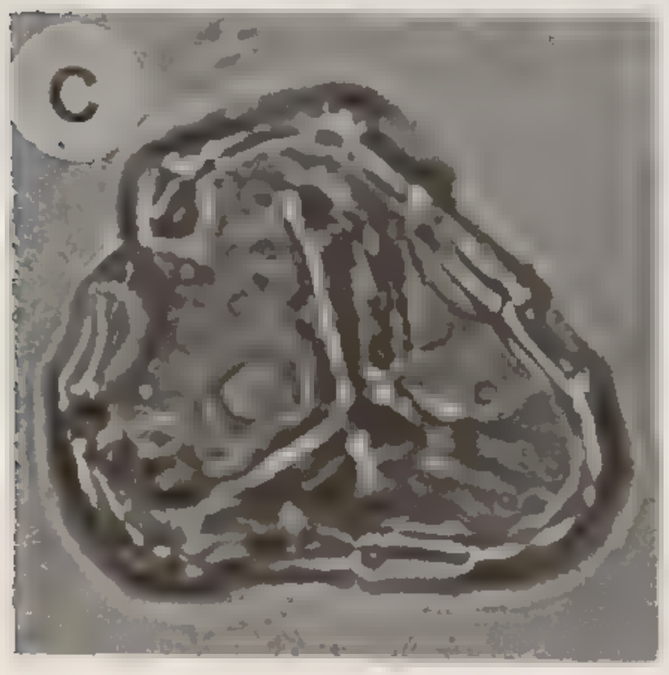
We confirm the spore morphology descriptions cited above, with one addition: In very rare cases some of the spores show more than three main pores (Fig. 2G). This is also true for fossil material (Fig. 2C).

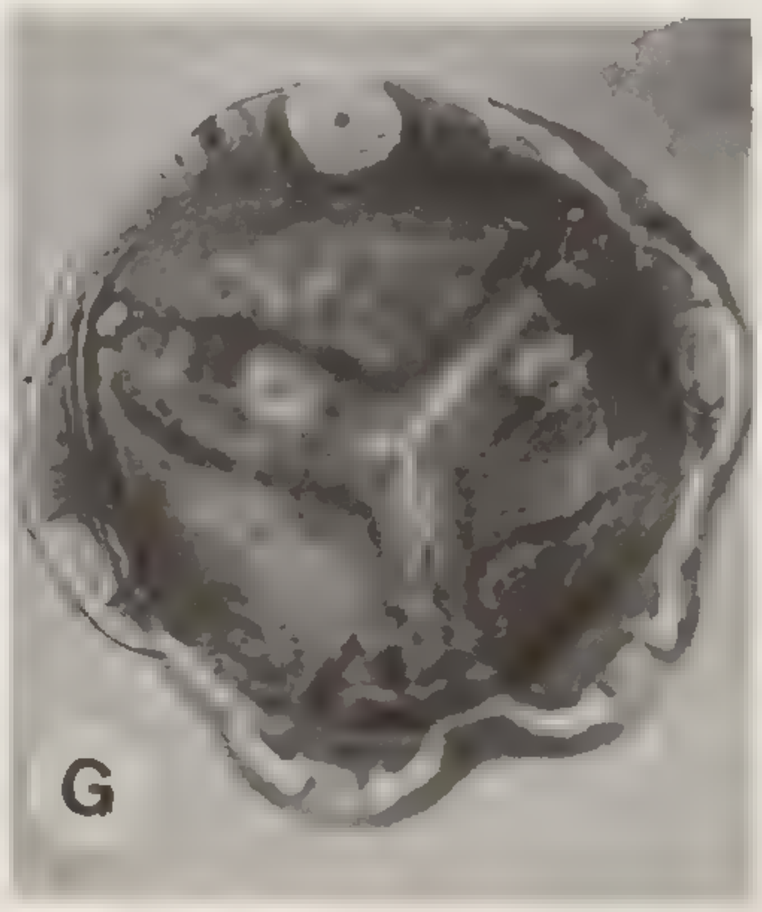
We show in this paper that the paleobiogeographic distribution pattern of *Kuylisporites waterbolkii* spores fits with the idea that *K. waterbolkii* is a spore belonging to an ancestral or closely related form of *Cnemidaria*. These ancestral species might have been a species of *Cyathea*, since many of the spores of *Cyathea* have a pitted exo-











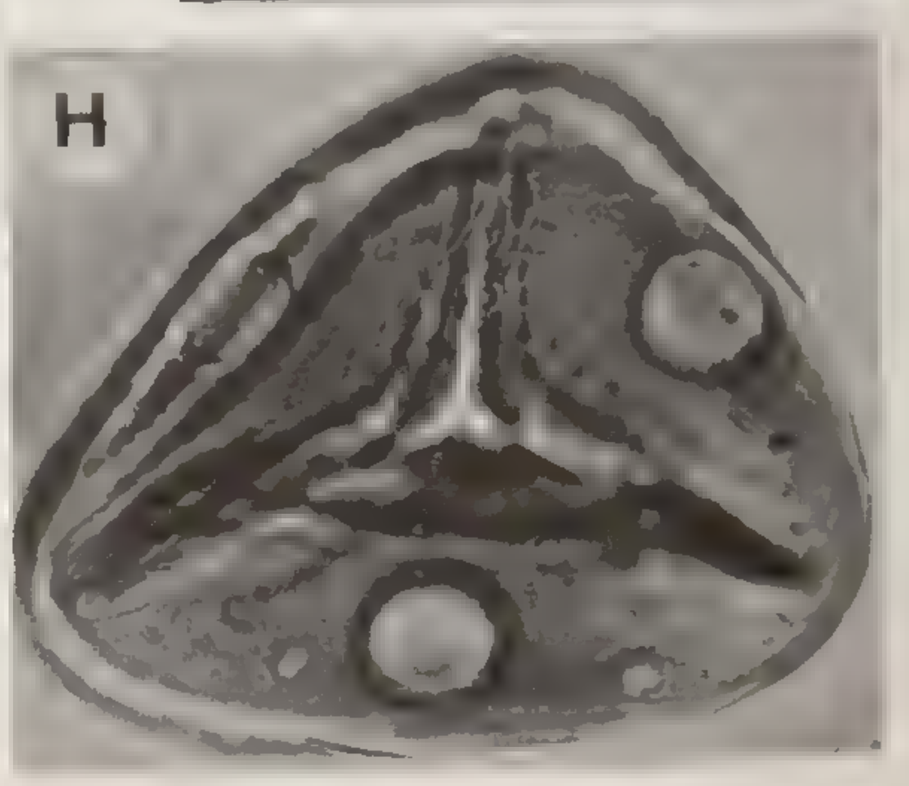


FIGURE 2. A. *Kuylisporites waterbolkii*; Sample 1578-59, 26–28 cm; Slide B, ×1000—B. *Kuylisporites waterbolkii*; Sample 1578-59, 123–125 cm, Slide D, ×1000.—C. *Kuylisporites waterbolkii*; Sample 1578-59, 26–28 cm; Slide B, ×1000.—D. *Cyatheacidites annulatus*; Sample 1578-59, 123–125 cm; Slide A, ×1000.—E. *Alsophila decurrens* var. *decurrens* Hook., Upolu (Samoa), *Sledge 1523*, × 250.—F. *Alsophila decurrens* var. *decurrens* Hook., Upolu (Samoa), *Sledge 1523*, ×1000.—G, H. *Cnemidaria horrida* (L.) Presl, Venezuela, *A. Smith 948*, ×1000.

spore. However, these pits are irregularly distributed and vary in size and are often obscured by a perispore. The similarity of the two spore-types is not surprising, because *Cyathea* and *Cnemidaria* are closely related. In fact, they are considered by some authors as subgenera (Kramer & Green, 1990) because of the presence of "intergeneric" hybrids (Holttum & Edwards, 1983).

PALEOBIOGEOGRAPHIC PATTERNS

The reported occurrences of species of *Kuylisporites* spores can be used to infer the paleobiogeographic history of this group. Equally important, however, is information on where they have not been found, since without such negative evidence, we cannot map the limits of its past distribution. Arguments based partly on negative evidence may be risky, as future discoveries may change an area of non-occurrence to one of occurrence. We have tried to minimize this possibility by considering *Kuylisporites* to be absent from a region only when there are well studied floras from the region. Based on this reasoning, a summary of the past geographic distribution of *Kuylisporites* is given in Table 1 and Figure 3. Table 1 is based on our knowledge of the palynological literature, although for reasons of space, we give and discuss citations only for cases of occurrence of *Kuylisporites*.

TABLE 1. Distribution of *Kuylisporites waterbolkii* (X) and *Kuylisporites* sp. (+) spores by geologic age and geographic area. Also shown is distribution of known floras which lack *Kuylisporites* (□). Dashes in Antarctica column indicate interval with no records due to continental glaciation.

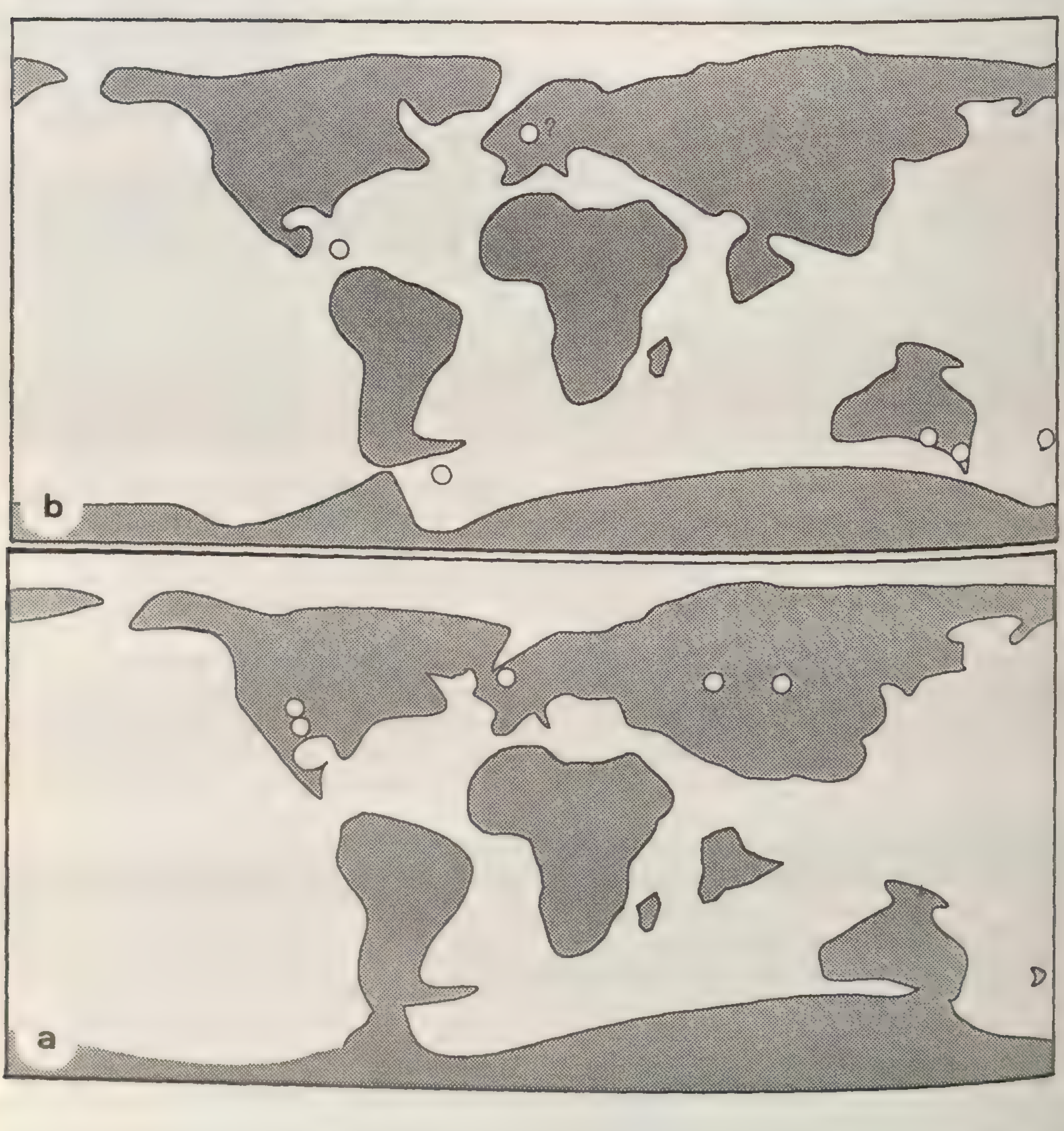
		Asia	Europe	North America	Central America	South America	Antarctica	Australia	New Zealand
Recent		□	□	□	✖	✖	—	□	□
Quaternary		□	□	□		✖	—	□	□
Pliocene		□	□	□	✖	✖	—	□	□
Miocene	L								
	M	□	□	□	✖		—	□	
	E				✖			✖	✖
Oligocene	L							✖	✖
		□	□	□	✖		□	✖	
	E							✖	
Eocene	L							✖	
	M		+?				✖	✖	✖
	E							✖	
Paleocene		+		+			□	□	□
Maastrichtian		+	+	+			□		
Pre-Maastr.		+	+	+			□		

Pre-Paleogene occurrences of *Kuylisporites* are known only from the Northern Hemisphere (Table 1, Fig. 3a). These spores, even though they resemble *K. waterbolkii* in their general aspect, are sufficiently different as to be considered directly ancestral or related to the genus *Cnemidaria*, i.e., most likely of cyatheaceous origin but not necessarily identical to *Cnemidaria*. True *Cnemidaria*-type spores (*K. waterbolkii*) are found from the mid-Eocene on exclusively in the most southerly palaeofloral province, the *Nothofagidites* province recognized in Australia, South America, and Antarctica (Table 1, Fig. 3b). The oldest strata containing *Cnemidaria*-type spores are of (late) early Eocene age from Australia (Stover & Partridge, 1973). The next oldest occurrences are those of the middle Eocene of the South Orkney Plateau, described in this paper, and the Oligocene occurrences of New Zealand (Pocknall & Mildenhall, 1984). The genus is not reported earlier than the Oligocene from the Caribbean (Puerto Rico).

Neogene occurrences of *Cnemidaria*-type spores (Table 1, Fig. 3c) are restricted to early Miocene localities in Australia and New Zealand (Stover & Partridge, 1973; Pocknall & Mildenhall, 1984), and several locations in the Caribbean, Central America, and northern South America.

This distribution pattern can be interpreted as follows: *Cnemidaria* sp. occurred at high southern latitudes from the Early Eocene through the Middle Eocene. Between the late Eocene and Oligocene, when dramatic cooling took place, caused by successive Antarctic glaciation, the genus migrated north. In Australia, where climatic deterioration was balanced by northward drift (Veevers et al., 1990), *Cnemidaria* persisted until the early Miocene. Increasing drought during the Neogene, however, led to its extinction there. In South America the distribution area shifted from high latitudes during the Eocene, when climatic conditions were warm-temperate, to low latitudes during the Oligocene, where *Cnemidaria* lived, and mostly still lives, in (sub)montane forests under tropical to temperate conditions. Only a few species, such as *C.*

c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spectabilis, are also occasionally found in the lowland forests of northern South America (Kramer, pers. comm.).

Kuylisporites has not been reported from South Africa (Coetzee et al., 1983, and literature cited there). The separation of South Africa from South America and Antarctica began as early as the late Jurassic. Antarctica had drifted far south by the early Cretaceous. The non-existence of *Cnemidaria* in South Africa is a strong hint that the genus must have spread over the Southern Hemisphere after Antarctica had drifted away from Africa—that is, not earlier than in the late Cretaceous.

Finally, the Quaternary distribution in Table 1 sheds light on on the possibility that *Cnemidaria*-type spores are present in other living species of Cyatheaceae, as not all have as yet been closely examined. Table 1 suggests that only those species which are today restricted to Central America and northern South America might possess such spores, as spores of this type are not reported from Quaternary to sub-Recent sediments elsewhere.

There is one exception to this argument. One other member of the genus *Alsophila* (Cyatheaceae), *Alsophila decurrens* var. *epaleata* Holttum, found on the Society Islands (Polynesia), exhibits similar wall structures (Tryon & Lugardon, 1991). We examined material in the collections of the Botanical Garden of Zürich (*Alsophila* (Cyathea) *decurrens* Hooker, *Sledge 1523*, Upolu, Samoa) and plates already published in the literature (Gastony & Tryon, 1976: 574). In addition, copies of SEM photographs, generously given by A. F. Tryon from *Alsophila decurrens* var. *epaleata* (collection of *Grant 5231*, Society Islands), were used for our studies. We note that in *A. decurrens* var. *decurrens* (Fig. 2E, F) the exospore seems to be smooth under the light microscope. Only SEM pictures reveal the microreticulate surface of the exospore (Gastony & Tryon, 1976). The 3-pitted spore type seems to occur only in *A. decurrens* var. *epaleata*. In *Cnemidaria*, the distinctive 3-pitted structures are uniformly developed, showing very little variation in morphology. In contrast, *A. decurrens* var. *epaleata* seems to have a relatively broad range of pore size ranging from big pores, like those seen in spores of *Cnemidaria*, to relatively small pores, not much bigger than those encountered in *A. decurrens* var. *decurrens*. In addition, Gastony & Tryon (1976) noted that in contrast to *Cnemidaria*, all the varieties of *Alsophila decurrens* seem to develop in the mature stage a perine layer around the exine. This fact and the range of morphologic variability, quite unlike *Cnemidaria*, suggest that the 3-pitted forms occasionally seen in *Alsophila* are only coincidentally similar to *Cnemidaria*, and are not truly homologous. Although the origin of pored spores in this species is of some evolutionary interest, the occurrence of 3-pitted spores in *Alsophila* does not appear to be directly related to the biogeographic history of *Cnemidaria* spores discussed in this paper.

We therefore conclude that the association of this distinctive spore's distribution in Quaternary sediments with the one widespread extant taxon known to possess this spore (*Cnemidaria*) supports the use of *Cnemidaria*-type spores as a tracer for the genus.

Conclusions

1. The cyatheaceous spore genus *Kuylisporites*, comprising four species, originated in the Northern Hemisphere in the late Cretaceous.

2. *Kuylisporites waterbolkii*, closely related to or identical with extant *Cnemidaria*, is known from the Early Eocene on. It was restricted to the Southern Hemisphere realm, where it shows a typical disjunct distribution, being absent from Africa. From the Middle Miocene on the biogeographic distribution of *K. waterbolkii* becomes gradually restricted to the area where *Cnemidaria* occurs today. Therefore, Central and South America and the Antilles might be considered a relict area for this genus.

3. Some fern taxa associated with *K. waterbolkii*, such as *Cyatheacidites annulatus* (*Lophosoria*, Lophosoriaceae), confirm the ecological interpretation of *K. waterbolkii* as an indicator of warm-temperate, not fully tropical climate. To remain in the same warm-temperate environment in which the *K. waterbolkii*-producing fern grew in southern high latitudes during the Paleogene, *Cnemidaria* migrated north when Antarctica became heavily glaciated during the Oligocene. Since

←

Figure 3. Location of *Cnemidaria* and *Cnemidaria*-like spores (o) on paleogeographic reconstructions created using Terra Mobilis program of Denham & Scotese (1987).—a. Cretaceous–Paleocene occurrences on a 68 Ma. map.—b. Eocene–Oligocene occurrences on a 45 Ma. map.—c. Neogene occurrences on a 15 Ma. map. More detailed information on localities is given in Table 1 and the Appendix.

most of the species of *Cnemidaria* seem to avoid fully tropical lowland habitats, *Cnemidaria* migrated in South America to higher elevations during the Neogene.

Literature Cited

Askin, R. A. 1989. Endemism and heterochroneity in the Late Cretaceous (Campanian) to Paleocene palynofloras of Seymour Island, Antarctica: Implications for origins, dispersal and palaeoclimates of southern floras. *In:* J. A. Crame (editor), Origins and Evolutions of the Antarctic Biota. Geol. Soc. Special Publ. 47: 107–119.

Barrera, E. & B. T. Huber. 1991. Paleogene and early Neogene oceanography of the southern Indian Ocean: Leg 119 foraminifer stable isotope results. Proc. Ocean Drilling Program, Sci. Results 119: 693–718.

Beeson, D. C. 1992. High Resolution Palynostratigraphy across a Marine Cretaceous–Tertiary Boundary Interval, Falls County, Texas. Ph.D. Thesis, Pennsylvania State University, University Park.

Berggren, W. A., D. V. Kent, J. J. Flynn & J. A. VanCouvering. 1985. Cenozoic geochronology. Geol. Soc. Amer. Bull. 96: 1407–1418.

Bolchovitina, N. A. 1953. Characteristics of spores and pollen in Cretaceous sediments of the central USSR. Sci. Acad. USSR, Geol. Ser. 61, Moskau. [In Russian.]

Bolli, H. M., J. B. Saunders & K. Perch-Nielsen. 1985. Plankton Stratigraphy. Cambridge Univ. Press, Cambridge.

Cassidy, D. S. (editor). 1980. Ara Islas Orcadas Cruise 1578, sediment descriptions. Antarctic Res. Facilities, Dept. Geol., Florida State Univ. Tallahassee, Sediment. Res. Lab. Contr. No. 48: 104.

Chlonova, A. F. 1960. Specific content of pollen and spores in Upper Cretaceous from the eastern part of the Western Siberian depression. Trudy Inst. Geol. Geophys., No. 3, Akad. Nauk. S.S.S.R. Novosibirsk 7. [In Russian.]

Coetzee, J. A., A. Scholtz & H. J. Deacon. 1983. Palynological studies and the vegetation history of the Fynbos. *In:* H. J. Deacon, Q. B. Hendey & J. J. N. Lambrechts (editors), Fynbos Ecology: A Preliminary Synthesis. South Africa National Scientific Programmes Report (CSIR) No. 75: 157–173.

Cookson, I. C. & M. E. Dettmann. 1958. Some trilete spores from Upper Mesozoic deposits in the eastern Australian region. Proc. Roy. Soc. Victoria 70: 95–128.

——— & K. Pike. 1954. The fossil occurrence of *Phyllocladus* and two other podocarpaceous types in Australia. Austral. J. Bot. 2: 60–68.

Copeland, E. B. 1930. Antarctica as the source of existing ferns. Proc. 6th Pacific Science Congress 4: 625–627.

Denham, C. R. & C. R. Scotese. 1987. Terra Mobilis: A Plate Tectonic Program for the Macintosh (computer program). Earth in Motion Technologies, Austin, Texas.

Dettmann, M. E. 1963. Upper Mesozoic microfloras from South-eastern Australia. Proc. Roy. Soc. Victoria 77: 1–148.

———. 1986. Significance of the Cretaceous–Tertiary spore genus *Cyatheacidites* in tracing the origin and migration of *Lophosoria* (Filicopsida). Special Pap. Palaeontol. 35: 63–94.

Engler, A. 1882. Versuch einer Entwicklungsgeschichte der extratropischen Florengebiete der südlichen Hemisphäre und der tropischen Gebiete. Engelmann, Leipzig.

Erdtman, G. & P. Sorsa. 1971. Pollen and Spore Morphology/Plant Taxonomy. Pteridophyta. Almqvist & Wiksell, Stockholm.

Evitt, W. R. 1973. Maestrichtian *Aquilapollenites* in Texas, Maryland, and New Jersey. Geoscience and Man 7: 31–38.

Gastony, G. J. & R. Tryon. 1976. Spore morphology in the Cyatheaceae 2. The genera *Lophosoria, Metaxya, Sphaeropteris, Alsophila* and *Nephelea.* Amer. J. Bot. 63: 738–758.

Graham, A. 1976. Studies in neotropical paleobotany. II. The Miocene communities of Veracruz, Mexico. Ann. Missouri Bot. Gard. 63: 787–842.

———. 1988. Lower Miocene floras and biogeography of Central America. J. Geol. Soc. Jamaica 25: 8–15.

———. 1991. Studies in neotropical paleobotany. VIII. The Pliocene communities of Panama—introduction and ferns, gymnosperms, angiosperms (Monocots). Ann. Missouri Bot. Gard. 78: 190–200.

——— & D. M. Jarzen. 1969. Studies in neotropical paleobotany. I. The Oligocene communities of Puerto Rico. Ann. Missouri Bot. Gard. 56: 308–357.

Hammen, T. van der & E. Gonzalez. 1960. Upper Pleistocene and Holocene climate and vegetation of the "Sabana de Bogota." Leidse Geol. Meded. 25: 261–315.

Holttum, R. E. & P. J. Edwards. 1983. The tree ferns of Mount Roraima and neighbouring areas of the Guayana Highlands with comments on the family Cyatheaceae. Kew. Bull. 38: 155–188.

Hooker, J. D. 1847. The Botany of the Antarctic voyage of H. M. discovery ships Erebus and Terror in the years 1839–1843. 1. Flora Antarctica. Reeve Bros., London. Reprinted 1963, J. Cramer, Weinheim.

Hsü, K. J., J. A. McKenzie, H. Oberhänsli, H. Weissert & R. C. Wright. 1984. South Atlantic Cenozoic Paleoceanography. *In:* K. J. Hsü, J. L. Labrecque et al., Initial Rep. Deep Sea Drilling Program 73: 771–785.

Kennett, J. P. & P. F. Barker. 1990. Latest Cretaceous to Cenozoic climate and oceanographic developments in the Weddell Sea, Antarctica: An ocean-drilling perspective. Proc. Ocean Drilling Program, Sci. Results 113: 937–960.

Kramer, K. U. & P. S. Green. 1990. The Families and Genera of Vascular Plants. I. Pteridophytes and Gymnosperms. Springer-Verlag, Berlin, Heidelberg.

Krutzsch, W. 1959. Mikropaläontologische (sporenpaläontologische) Untersuchungen in der Braunkohle des Geiseltales. Geologie 8(21–22): 1–425.

Kuyl, O. S., J. Muller & H. Th. Waterbolk. 1955. The application of palynology to oil geology with reference to western Venezuela. Geol. en Mijnbouw 17: 49–76.

Lellinger, D. B. 1975. A phytogeographic analysis of Choco pteridophytes. Fern Gaz. 11: 105–114.

Macphail, M. K. & E. M. Truswell. 1989. Palynostratigraphy of the central west Murray Basin. Bur. Mineral Resources, Geol. & Geophys., J. Austral. Geol. & Geophys. 11: 301–331.

Mägdefrau, K. 1960. Vom Orinoko zu den Anden. Vierteljahrsschr. Naturf. Ges. Zürich 105: 49–71.

Mao, S. & B. A. R. Mohr. (in press). Middle Eocene dinocysts from South Scotia Ridge (Antarctica) and their palaeoclimatic implications. Rev. Palaeobot. Palynol.

Mohr, B. A. R. 1990. Eocene and Oligocene sporomorphs and dinoflagellate cysts from Leg 113 drill sites, Weddell Sea, Antarctica. Proc. Ocean Drilling Programs, Sci. Results 113: 295–612.

Moran, R. C. 1990. Two new species of *Cnemidaria* (Cyatheaceae) from Panama. Ann. Missouri Bot. Gard. 77: 246–248.

Newman, K. R. 1964. Palynologic correlations of Late Cretaceous and Paleocene formations, north-western Colorado. Soc. Econ. Paleontol. & Mineral., Special Publ. 11: 169–180.

———. 1965. Upper Cretaceous–Paleocene guide palynomorphs from Northwestern Colorado. Univ. Colorado Stud., Ser. Earth Sci. 4(2).

Pocknall, D. T. & D. C. Mildenhall. 1984. Late Oligocene–early Miocene spores and pollen from Southland, New Zealand. New Zealand Geol. Surv. Palaeontol. Bull. 51: 1–66.

Potonié, R. 1956. Synopsis der Gattungen der Sporae dispersae. 1. Sporites. Beih. Geol. Jahrb. 23: 1–103.

Stolze, R. G. 1974. Taxonomic revision of the genus *Cnemidaria* (Cyatheaceae). Fieldiana (Bot.) 37: 1–96.

Stott, L. D. & J. P. Kennett. 1990. Antarctic Paleogene planktonic Foraminifer biostratigraphy: ODP Leg 113, Sites 689 and 690. Proc. Ocean Drilling Program, Sci. Results 113: 549–569.

Stover, L. E. & P. R. Evans. 1973. Upper Cretaceous–Eocene spore-pollen zonation, offshore Gippsland Basin, Australia. Special Publ. Geol. Soc. Austral. 4: 55–72.

——— & A. D. Partridge. 1973. Tertiary and Late Cretaceous spores and pollen from the Gippsland Basin, Southeastern Australia. Proc. Roy. Soc. Victoria 85: 237–286.

Thomas, E. 1990. Late Cretaceous through Neogene deep-sea benthic foraminifers (Maud Rise, Weddell Sea, Antarctica). Proc. Ocean Drilling Program, Sci. Results 113: 571–594.

Toker, V., P. F. Barker & S. W. Wise, Jr. 1991. Middle Eocene carbonate-bearing marine sediments from Bruce Bank off the northern Antarctic Peninsula. Pp. 639–644 *in* J. W. Thomson et al. (editors), Evolution of Antarctica. Proc. 5th Internat. Symp. Antarctic Earth Sci., Cambridge 1987, Cambridge Univ. Press, Cambridge.

Tryon, A. F. & B. Lugardon. 1991. Spores of the Pteridophyta. Springer, New York, Berlin.

Tryon, R. M. & A. F. Tryon. 1982. Ferns and Allied Plants with Special Reference to Tropical America. Springer, New York, Berlin.

Veevers, J. J., H. M. J. Stagg, J. B. Willcox & H. L. Davies. 1990. Pattern of slow seafloor spreading (less than 4 mm/year) from breakup (96 Ma) to A20 (44.5 Ma) off the southern margin of Australia. Bur. Mineral Resources, Geol. & Geophys., J. Austral. Geol. & Geophys. 11: 499–507.

Wegener, A. 1926. Paläogeographische Darstellung der Theorie der Kontinentalverschiebungen. Pp. 174–189 *in* O. Kende (editor), Enzyklopedie der Erdkunde. Deuticke, Leipzig, Wien.

Appendix. Occurrences and publications of *Kuylisporites* sp.

1953 *Hemitelia mirabilis* Bolkhovitina: Bolkhovitina (1953: 47, pl. 6, fig. 10); Cenomanian of USSR, eastern slope of the South-Ural, near Nowo-Nikolaewskogo.

1955 Cyatheaceae (*Hemitelia* type): Kuyl, Muller & Waterbolk (1955: pl. 1, fig. 7); late Tertiary of Trinidad.

1956 *Kuylisporites waterbolkii* Potonié: Potonié (1956: 103, pl. 4, fig. 39).

1959 *Kuylisporites mirabilis* (Bolkhovitina) Krutzsch: Krutzsch (1959: 190), based on *Hemitelia mirabilis*, published by Bolkhovitina in 1953.

1960 *Kuylisporites separatus* Chlonova: Chlonova (1960: 11, pl. 1, figs. 6 and 7); Maastrichtian and Paleocene of western Siberia.

1960 *Hemitelia*: van der Hammen & Gonzalez (1960: 296, pl. 16, fig. 126); Quaternary of Colombia, perhaps reworked.

1961 *Kuylisporites* (cf. *Hemitelia*) sp.: Samoilovitch et al. (1961: pl. 79, fig. 4); Maastrichtian of the USSR (citation from Dettmann, 1963).

1964 *Kuylisporites* sp.: Newman (1964: 174, pl. 1, fig. 4); late Cretaceous of Colorado.

1965 *Kuylisporites scutatus* Newman: Newman (1965: 9, pl. 1, fig. 1); Campanian of northwestern Colorado.

1969 *Hemitelia* (*Cnemidaria*): Graham & Jarzen (1969: 317, fig. 9); Oligocene of Puerto Rico.

1973 *Kuylisporites scutatus* Newman: Evitt (1973: 33, pl. 1, fig. 19); Maastrichtian and Paleocene of Texas.

1973 *Kuylisporites waterbolkii* Potonié: Stover & Evans (1973: pl. 3, fig. 13); late early Eocene to late Eocene off southeastern Australia.

1973 *Kuylisporites waterbolkii* Potonié: Stover & Partridge (1973: 249); early Eocene to early Miocene of southeastern Australia.

1976 *Hemitelia*: Graham (1976: 812, figs. 23, 24); Miocene of Mexico.

1984 *Kuylisporites waterbolkii* Potonié: Pocknall & Mildenhall (1984: 20 pl. 2, fig. 6); late Oligocene to early Miocene of New Zealand.

1988 *Cnemidaria*: Graham (1988: 10, 11); early Miocene of Costa Rica.

1989 *Kuylisporites waterbolkii* Potonié: Macphail & Truswell (1989: 330); late Eocene to early late Oligocene, Murray Basin, southeastern Australia.

1991 *Cnemidaria*: Graham (1991: 193, 194, figs. 12, 13); Pliocene of Panama.

1994 *Kuylisporites waterbolkii* Potonié: Mohr & Lazarus (1994, this paper); mid-Eocene, Bruce Bank, South Orkney area.

CHROMOSOME NUMBERS IN BOLIVIAN GRASSES (GRAMINEAE)[1]

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ABSTRACT

Chromosome numbers are reported for 59 collections of grasses from Bolivia representing 43 species and 21 genera. First chromosome counts are reported for the following six species: *Imperata tenuis*, $2n = 20$; *Paspalum acuminatum*, $2n = 40$; *P. kempffii*, $2n = 40$; *P. lenticulare*, $2n = 40$; *P. lineare*, $2n = 80$; *P. macedoi*, $2n = 40$. Counts differing from previously reported numbers are given for the following five species: *Gymnopogon spicatus*, $2n = 40$; *Leersia hexandra*, $2n = 72$; *Pennisetum setosum*, $2n = 45$; *Setaria vulpiseta*, $2n = 54$; *Thrasya petrosa*, $2n = 20$.

Information on chromosome numbers in carefully vouchered specimens is of fundamental importance in understanding plant phylogeny, particularly in regard to polyploid taxa (Raven, 1975; Davidse et al., 1986). An understanding of the relationships between polyploidy and apomixis in several tropical grass genera (e.g., *Paspalum*, *Panicum*, *Dichanthium*, *Bothriochloa*, and *Brachiaria*) is required by plant breeders and other investigators studying plant reproductive biology (Connor, 1979; Quarín & Norrmann, 1987). Numerous chromosome counts have been obtained over the past 30 years; nonetheless, species native to certain geographic regions, such as central South America, remain virtually unstudied. Chromosome numbers for Bolivian grasses have been reported only by two studies; Bowden & Senn (1962) reported counts for 10 species from the eastern lowlands, while Killeen (1990) obtained meiotic counts for 32 genera and 48 species from the Brazilian Shield region of Santa Cruz. This paper provides complementary information to Killeen's (1990) study.

Chromosome counts were determined to be new or different by comparison to Killeen (1990), Honfi et al. (1990), and Dubcosky & Zuloaga (1991) or, where not specifically cited, from the summary listings of Darlington & Wylie (1956), Ornduff (1967, 1968, 1969), Fedorov (1969), Moore (1973, 1977), Goldblatt (1981, 1984, 1985, 1988), and Goldblatt & Johnson (1990).

MATERIALS AND METHODS

Plants were obtained from seed collected by Killeen in natural populations in eastern lowland Bolivia. Most accessions originated from the Brazilian Shield region of Santa Cruz (i.e., Prov. Ñuflo de Chávez), but several species were collected from the sand savannas of the piedmont in western Santa Cruz (Prov. Andrés Ibáñez) or the inundated savannas of the western Beni (Table 1).

Chromosome counts were made from mitotic squashes of root-tips collected from potted plants. Root-tips were collected between 8:00 and 10:00 A.M. and pretreated for two hours with alpha-bromonaftalene at room temperature. Subsequently, the material was hydrolyzed with a 1 N solution of HCl at 60°C for ten minutes and stained with fuchsin; squashes were made with a drop of ■ceto orcein. An average of three plants per accession were scored. A complete list of species, voucher specimens for individual accessions, and locality data is provided in Table 1; a list of synonyms is provided by Killeen (1990). Replicate specimens of all accessions cited in Table 1 have been deposited at CTES and ISC; partial sets of Killeen collections are at LPB, MO, SI, US, and USZ.

RESULTS AND DISCUSSION

This paper presents the chromosome numbers, as determined by mitotic divisions, for 59 separate

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TABLE 1. Zygotic chromosome number ($2n$), locality of origin, and collection number of 43 Bolivian grass species.

Species	$2n$	Origin, voucher, and figure references
Andropogon lateralis Nees	60	Dept. Santa Cruz: Prov. Andrés Ibáñez, Pampa Viru Viru, 1 km E of the International Airport, 17°40′S, 63°10′W, 400 m, *Killeen 1550*
Arundinella hispida (Willd.) Kuntze	20	Dept. Beni: Prov. Ballivian, Estación Biológica del Beni, Estancia Porvenir, 40 km E of San Borja, 14°35′S, 66°30′W, 200 m, *Killeen 2593* (Fig. 1)
Axonopus chrysoblepharis (Lag.) Chase	20	Dept. Santa Cruz: Prov. Ñuflo de Chávez, Pueblo de Concepción on road around reservoir, 16°03′S, 62°10′W, 500 m, *Killeen 2011A*
Axonopus compressus (Sw.) P. Beauv.	40	Dept. Santa Cruz: Prov. Ñuflo de Chávez, Estancia Las Madres, 9 km N of Concepción, 16°00′S, 62°00′W, 500 m, *Killeen 1751*
Axonopus fissifolius (Raddi) Kuhlm.	20	Dept. Santa Cruz: Prov. Ñuflo de Chávez, Estancia Viera, 2 km S of Concepción, 16°08′S, 62°05′W, 500 m, *Killeen 2275*
Elionurus muticus (Spreng.) Kuntze	20	Dept. Santa Cruz: Prov. Ñuflo de Chávez, Estancia Santa María, 10 km S of Concepción on road to Lomerío, 16°13′S, 62°00′W, 500 m, *Killeen 2187*
Eriochloa distachya HBK	18	Dept. Santa Cruz: Prov. Ñuflo de Chávez, Estancia Santa María, 7 km S of Concepción on road to Lomerío, 16°10′S, 62°00′W, 500 m, *Killeen 2441*
Gouinia virgata (C. Presl) Scribn.	40	Dept. Santa Cruz: Prov. Ñuflo de Chávez, 17 km N of Concepción on road to San Ignacio, 15°50′S, 62°00′W, 400 m, *Killeen 1885*
Gymnopogon spicatus (Spreng.) Kuntze	40**	Dept. Santa Cruz: Prov. Ñuflo de Chávez, 3 km S of Concepción on road around reservoir, 16°03′S, 62°10′W, 500 m, *Killeen 2017*
Imperata tenuis Hack.	20*	Dept. Santa Cruz: Prov. Ñuflo de Chávez, Estancia Santa María, 10 km S of Concepción on road to Lomerío, 16°13′S, 62°00′W, 500 m, *Killeen 2482* (Fig. 2)
Lasiacis sorghoidea (Desv.) Hitchc.	36	Dept. Santa Cruz: Prov. Ñuflo de Chávez, Rancho Puesto Nuevo, 40 km S of Concepción on road to Lomerío, 16°25′S, 62°00′W, 700 m, *Killeen 2332* (Fig. 3)
Leersia hexandra Sw.	72**	Dept. Santa Cruz: Prov. Ñuflo de Chávez, Estancia Viera, 2 km S of Concepción, 16°08′S, 62°05′W, 480 m, *Killeen 2416*
Microchloa indica (L. f.) P. Beauv.	12	Dept. Santa Cruz: Prov. Ñuflo de Chávez, Comunidad Puesto Nuevo, 60 km S of Concepción on road to Lomerío, 16°25′S, 62°00′W, 450–700 m, *Killeen 1826*
Oryza rufipogon Griffith	24	Dept. Santa Cruz: Prov. Ñuflo de Chávez, Estancia Santa María, 8 km S of Concepción on road to Lomerío, 16°10′S, 62°00′W, 500 m, *Killeen 2086*
Panicum laxum Sw.	40	Dept. Santa Cruz: Prov. Andrés Ibáñez, Pampa Viru Viru, 1 km E of International Airport, 17°40′S, 63°10′W, 400 m, *Killeen 1554*
Panicum laxum Sw.	40	Dept. Santa Cruz: Prov. Ñuflo de Chávez, Estancia Salta, 10 km S of Concepción on road to Lomerío, 16°13′S, 62°00′W, 500 m, *Killeen 2286* (Fig. 4)
Panicum mertensii Roth ex Roem. & Schult.	36	Dept. Santa Cruz: Prov. Ñuflo de Chávez, 20 km W of Santa Rosa de la Roca on road to San Ignacio, 15°50′S, 61°40′W, 300 m, *Killeen 1745*
Panicum olyroides HBK	36	Dept. Santa Cruz: Prov. Ñuflo de Chávez, Estancia El Recreo, 2 km N of Concepción, 16°02′S, 62°08′W, 480 m, *Killeen 2398* (Fig. 5)
Panicum trichanthum Nees	36	Dept. Santa Cruz: Prov. Andrés Ibáñez, Pampa Viru Viru, 1 km E of the International Airport, 17°40′S, 63°10′W, 400 m, *Killeen 1556*

TABLE 1. Continued.

Species	2*n*	Origin, voucher, and figure references
Paspalum acuminatum Raddi	40*	Dept. Santa Cruz: Prov. Ñuflo de Chávez, Estancia San Sebastián, 25 km S of Concepción on road to Lomerío, 16°20′S, 62°00′W, 500 m, *Killeen 2325*
Paspalum erianthum Nees ex Trin.	80	Dept. Santa Cruz: Prov. Ñuflo de Chávez, Estancia Salta, 10 km S of Concepción on road to Lomerío, 16°13′S, 62°00′W, 460 m, *Killeen 1194*
Paspalum erianthum Nees ex Trin.	80	Dept. Santa Cruz: Prov. Ñuflo de Chávez, Estancia Santa María, 10 km S of Concepción on road to Lomerío, 16°13′S, 62°00′W, 500 m, *Killeen 2191*
Paspalum guenoarum Arechav.	40	Dept. Santa Cruz: Prov. Ñuflo de Chávez, Estancia El Recreo, 2 km N of Concepción, 16°13′S, 62°00′W, 500 m, *Killeen 2390*
Paspalum guenoarum Arechav.	40	Dept. Santa Cruz: Prov. Ñuflo de Chávez, Estancia El Recreo, 2 km N of Concepción, 16°13′S, 62°00′W, 500 m, *Killeen 2394* (Fig. 6)
Paspalum humigenum Swallen	20	Dept. Santa Cruz: Prov. Ñuflo de Chávez, Estancia La Pachanga, 5 km S of Concepción on road to Lomerío, 16°08′S, 62°05′W, 500 m, *Killeen 2246*
Paspalum intermedium Munro ex Morong & Britton	40	Dept. Santa Cruz: Prov. Ñuflo de Chávez, Estancia Viera, 2 km S of Concepción on road to Lomerío, 16°08′S, 62°05′W, 500 m, *Killeen 1631*
Paspalum intermedium Munro ex Morong & Britton	40	Dept. Santa Cruz: Prov. Ñuflo de Chávez, Estancia La Pachanga, 5 km S of Concepción on road to Lomerío, 16°08′S, 62°00′W, 500 m, *Killeen 2258*
Paspalum kempffii Killeen	40*	Dept. Santa Cruz: Prov. Ñuflo de Chávez, Estancia La Pachanga, 5 km S of Concepción on road to Lomerío, 16°13′S, 62°05′W, 500 m, *Killeen 2272*
Paspalum lenticulare HBK	40*	Dept. Santa Cruz: Prov. Andrés Ibáñez, Pampa Viru Viru, 1 km E of International Airport, 17°40′S, 63°10′W, 400 m, *Killeen 1557*
Paspalum lenticulare HBK	40	Dept. Santa Cruz: Prov. Ñuflo de Chávez, Estancia Salta, 10 km S of Concepción on road to Lomerío, 16°10′S, 62°05′W, 500 m, *Killeen 2270*
Paspalum lenticulare HBK	40	Dept. Santa Cruz: Prov. Ñuflo de Chávez, Estancia San Sebastián, 25 km S of Concepción on road to Lomerío, 16°20′S, 62°00′W, 500 m, *Killeen 2322*
Paspalum lenticulare HBK	40	Dept. Santa Cruz: Prov. Ñuflo de Chávez, Estancia El Recreo, 2 km N of Concepción, 16°13′S, 62°00′W, 500 m, *Killeen 2396*
Paspalum limbatum Henrard	20	Dept. Santa Cruz: Prov. Ñuflo de Chávez, Estancia Viera, 2 km S of Concepción on road to Lomerío, 16°13′S, 62°05′W, 500 m, *Killeen 1622*
Paspalum limbatum Henrard	20	Dept. Santa Cruz: Prov. Ñuflo de Chávez, Estancia La Pachanga, 5 km S of Concepción on road to Lomerío, 16°08′S, 62°05′W, 500 m, *Killeen 2276*
Paspalum limbatum Henrard	20	Dept. Santa Cruz: Prov. Ñuflo de Chávez, Estancia Salta, 10 km S of Concepción on road to Lomerío, 16°08′S, 62°00′W, 500 m, *Killeen 2453* (Fig. 7)
Paspalum lineare Trin.	80*	Dept. Santa Cruz: Prov. Ñuflo de Chávez, Estancia La Pachanga, 5 km S of Concepción on road to Lomerío, 16°08′S, 62°05′W, 500 m, *Killeen 2218*
Paspalum macedoi Swallen	40*	Dept. Santa Cruz: Prov. Ñuflo de Chávez, Estancia Las Madres, 9 km N of Concepción on road to San Ignacio, 16°00′S, 62°00′W, 500 m, *Killeen 1796*
Paspalum maculosum Trin.	40	Dept. Santa Cruz: Prov. Ñuflo de Chávez, Estancia Salta, 10 km S of Concepción on road to Lomerío, 16°13′S, 62°00′W, 500 m, *Killeen 2282* (Fig. 8)

TABLE 1. Continued.

Species	2*n*	Origin, voucher, and figure references
Paspalum malacophyllum Trin.	40	Dept. Santa Cruz: Prov. Ñuflo de Chávez, Estancia San Josecito, 8 km S de Concepción on road to Lomerío, 16°02′S, 62°05′W, 490 m, *Killeen 1918*
Paspalum malacophyllum Trin.	40	Dept. Santa Cruz: Prov. Ñuflo de Chávez, Estancia El Recreo, 2 km N of Concepción, 16°12′S, 62°08′W, 500 m, *Killeen 2449*
Paspalum minus E. Fourn.	50	Dept. Santa Cruz: Prov. Andrés Ibáñez, Pampa Viru Viru, 1 km E of the International Airport, 17°40′S, 63°10′W, 500 m, *Killeen 1584*
Paspalum plenum Chase	40	Dept. Santa Cruz: Prov. Ñuflo de Chávez, Estancia Viera, 2 km SE of Concepción, 16°13′S, 62°00′W, 500 m, *Killeen 2317*
Paspalum plicatulum Michx.	40	Dept. Santa Cruz: Prov. Ñuflo de Chávez, Estancia La Pachanga, 5 km S of Concepción on road to Lomerío, 16°08′S, 62°05′W, 480 m, *Killeen 2444*
Paspalum plicatulum Michx.	40	Dept. Santa Cruz: Prov. Ñuflo de Chávez, Estancia Salta, 10 km S of Concepción on road to Lomerío, 16°13′S, 62°00′W, 500 m, *Killeen 2455*
Pennisetum setosum (Sw.) Rich.	45**	Dept. Santa Cruz: Prov. Ñuflo de Chávez, Comunidad Puesto Nuevo, 30 km S of Concepción on road to Lomerío, 16°25′S, 62°00′W, 700 m, *Killeen 1821*
Pharus lappulaceus Aubl.	24	Dept. Santa Cruz: Prov. Ñuflo de Chávez, 17 km S of Concepción on Road to San Ignacio, 15°50′S, 62°00′W, 400 m, *Killeen 1890*
Saccharum trinii Hack.	60	Dept. Santa Cruz: Prov. Ñuflo de Chávez, Estancia La Pachanga, 5 km S of Concepción on road to Lomerío, 16°08′S, 62°05′W, 500 m, *Killeen 2219*, chasmogamous form
Saccharum trinii Hack.	60	Dept. Santa Cruz: Prov. Ñuflo de Chávez, Estancia Salta, 10 km S of Concepción, 16°13′S, 62°00′W, 500 m, *Killeen 2281*, cleistogamous form
Schizachyrium sanguineum (Retz.) Alston	50	Dept. Santa Cruz: Prov. Andrés Ibáñez, Pampa Viru Viru, 1 km E of the International Airport, 17°40′S, 63°10′W, 400 m, *Killeen 1551*
Schizachyrium sanguineum (Retz.) Alston	50	Dept. Santa Cruz: Prov. Ñuflo de Chávez, Pueblo de Concepción, the laguna west of town, 16°05′S, 62°00′W, 500 m, *Killeen 1851*
Schizachyrium sanguineum (Retz.) Alston	60	Dept. Santa Cruz: Prov. Ñuflo de Chávez, Pueblo de Concepción, the laguna west of town, 16°05′S, 62°00′W, 500 m, *Killeen 2026*
Schizachyrium sanguineum (Retz.) Alston	70	Dept. Santa Cruz: Prov. Ñuflo de Chávez, Pueblo de Concepción, the laguna west of town, 16°05′S, 62°00′W, 500 m, *Killeen 2026*
Schizachyrium sanguineum (Retz.) Alston	60	Dept. Santa Cruz: Prov. Ñuflo de Chávez, Estancia Salta, 10 km S of Concepción, 16°13′S, 62°00′W, 500 m, *Killeen 2095* (Fig. 9)
Setaria parviflora (Poir.) Kerguélen	36	Dept. Santa Cruz: Prov. Ñuflo de Chávez, Estancia Salta, 10 km S of Concepción on road to Lomerío, 16°13′S, 62°00′W, 500 m, *Killeen 2273*
Setaria vulpiseta (Lam.) Roem. & Schult.	54**	Dept. Santa Cruz: Prov. Ñuflo de Chávez, Estancia San Sebastián, 25 km S of Concepción on road to Lomerío, 16°20′S, 62°00′W, 500 m, *Killeen 2318* (Fig. 10)
Sorghastrum minarum (Nees) Hitchc.	20	Dept. Santa Cruz: Prov. Ñuflo de Chávez, Estancia El Recreo, 2 km N of Concepción, 16°02′S, 62°08′W, 480 m, *Killeen 2387*
Sorghastrum setosum (Griseb.) Hitchc.	20	Dept. Santa Cruz: Prov. Ñuflo de Chávez, Estancia Salta, 10 km S of Concepción on road to Lomerío, 16°13′S, 62°00′W, 500 m, *Killeen 2306* (Fig. 11)

TABLE 1. Continued.

Species	2*n*	Origin, voucher, and figure references
Thrasya crucensis Killeen	20	Dept. Santa Cruz: Prov. Ñuflo de Chávez, Comunidad Puesto Nuevo, 40 km S of Concepción on road to Lomerío, 16°25′S, 62°00′W, 700 m, *Killeen 2334*
Thrasya petrosa (Trin.) Chase	40	Dept. Santa Cruz: Prov. Ñuflo de Chávez, Estancia Salta, 10 km S of Concepcíon on road to Lomerío, 16°13′S, 62°00′W, 500 m, *Killeen 1953*
Thrasya petrosa (Trin.) Chase	20**	Dept. Santa Cruz: Prov. Ñuflo de Chávez, Estancia Viera, 2 km S of Concepción on road to Lomerío, 16°08′S, 62°05′W, 500 m, *Killeen 2418*

* First count for this taxon.
** Count different from previous ones for this taxon.

accessions of 43 species in 21 genera and seven tribes of Gramineae. Chromosome counts for six species are reported for the first time, while an additional five species were discovered to have chromosome numbers different from those previously reported. The results of mitotic counts are presented in Table 1; selected squashes are presented in Figures 1–11. Selected species are discussed in detail in the following paragraphs.

Arundinella hispida was documented as $2n = 20$ (Fig. 1) in agreement with a previous report by Gould & Soderstrom [1967, sub *Arundinella confinis* (Schult.) Hitchc. & Chase].

An accession of *Gymnopogon spicatus* was documented as being tetraploid ($2n = 40$, for *Killeen 2017*), which contrasts to the diploid accession (*Killeen 2481*) reported by Killeen (1990). The two accessions were collected within 5 km of one another near the village of Concepción.

Imperata tenuis was documented as a diploid with $2n = 20$ (Fig. 2); this is the first chromosome count for the species. The base of $x = 10$ conforms with other reports for the genus.

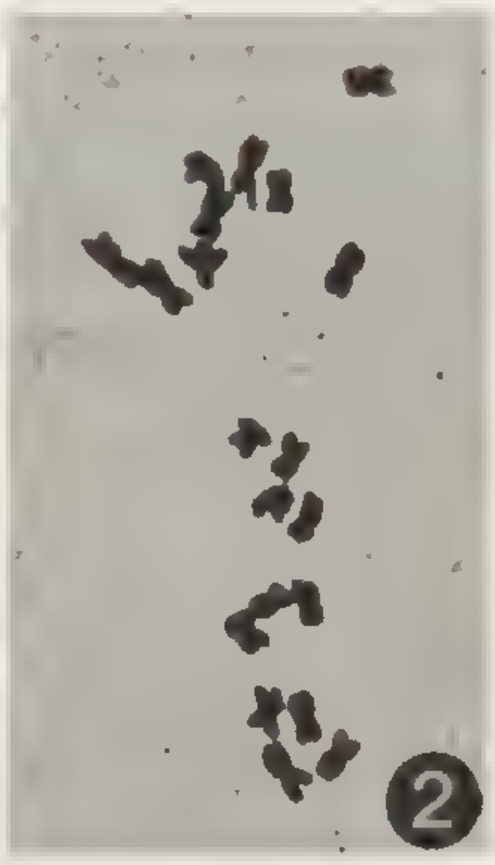
Leersia hexandra is a pantropical species, and since Ramiah (1935) numerous investigators have reported it as uniformly $2n = 48$. Surprisingly, the same population near Concepción (voucher *Killeen 2416*) was found to contain both hexaploid plants ($2n = 72$) by the mitotic counts reported here, as well as tetraploid plants ($2n = 48$) by the meiotic preparations previously reported by Killeen (1990).

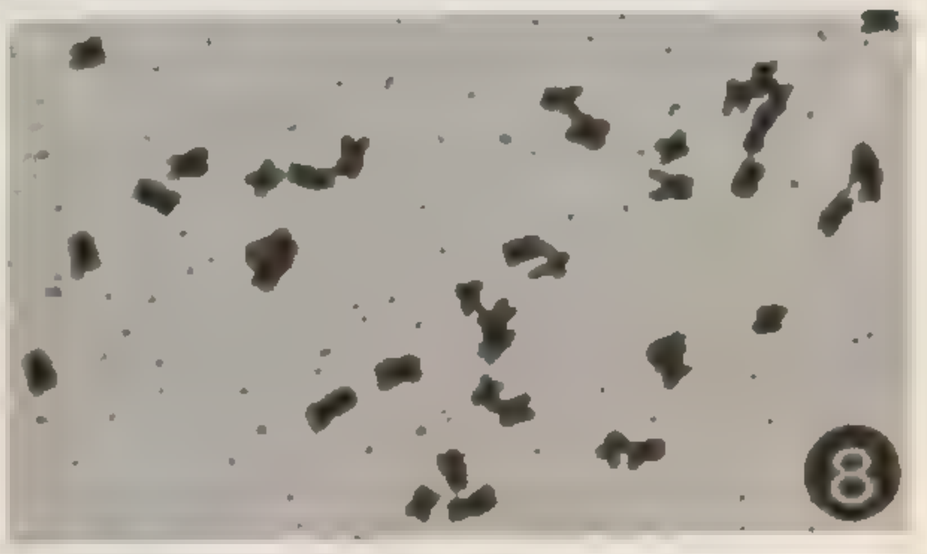
Paspalum is the most speciose grass genus in the Neotropics and is, likewise, the most abundant genus in eastern lowland Bolivia. Consequently, most of the counts reported here belong to this genus. New counts are reported for *P. acuminatum*, *P. macedoi*, *P. kempffii*, and *P. lenticulare*, all of which are $2n = 40$, as well as for *P. lineare*, which is $2n = 80$.

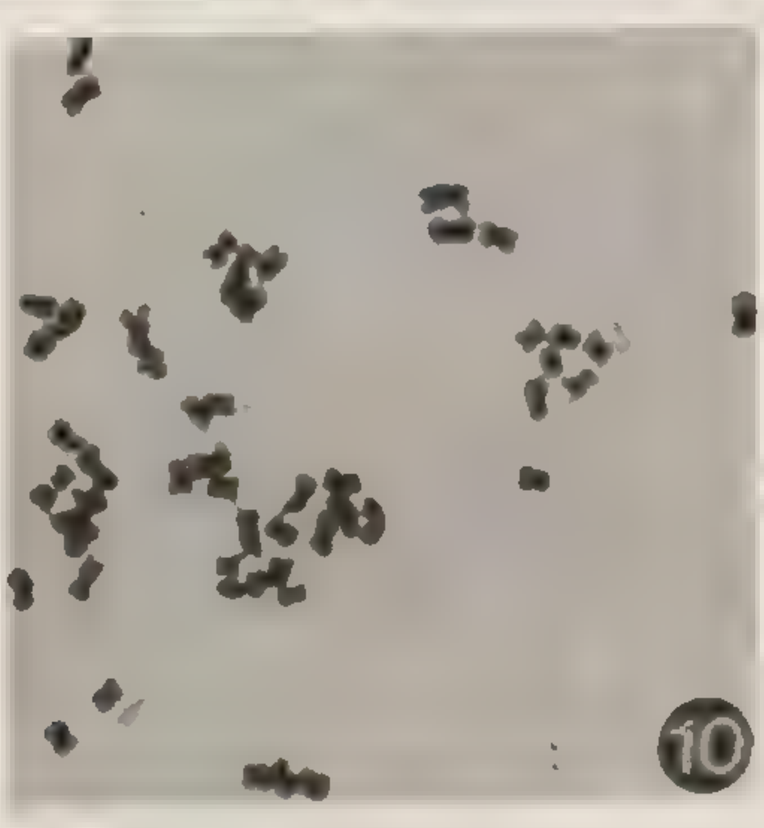
Pennisetum setosum is a neotropical species with previous counts of $2n = 36$, 72, and 54 chromosomes; this is the first report of a pentaploid $2n = 45$ cytotype. Nonetheless, plants were relatively fecund in natural populations, and plants raised in cultivation at Corrientes were fully fertile. Presumably the species, or at least this accession, reproduces via apomixis, a phenomenon that has been reported for the genus (Dujardin & Hanna, 1984).

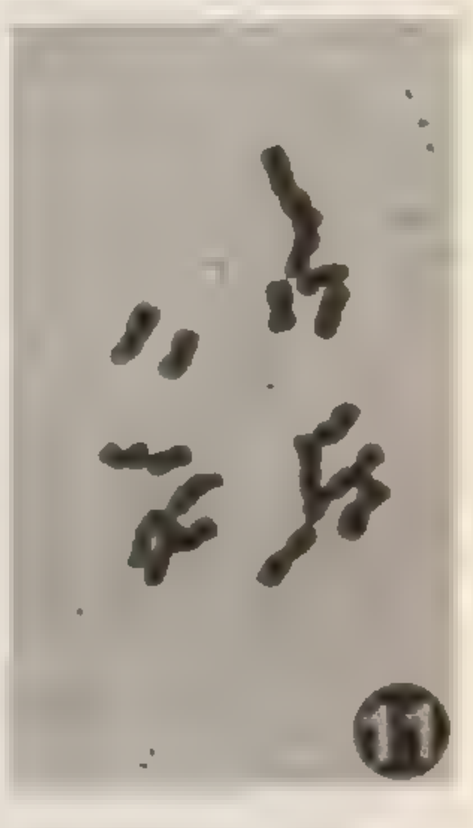
This is the first reliable count for *Saccharum trinii*. A previous study reported that $2n$ was about 60 (Molina, 1981), and that figure has been verified by this study. Killeen (1990) reported that this species existed as two intergrading phenological phenotypes. Early-blooming chasmogamy was induced by fire, while late-blooming cleistogamy occurred in nonburned individuals. Both phenotypes were documented as $2n = 60$ cytotypes (Table 1).

Schizachyrium sanguineum is a morphologically and cytologically variable taxon with a pantropical distribution. Populations range from diploid to decaploid in different floras of the world. Neotropical variants have traditionally been recognized as *S. hirtiflorum* Nees or *S. semiberbis* Nees based on spikelet characteristics. The cytological information reported here reinforces the view that *S. sanguineum* (sensu lato) is best viewed as a complex of morphologically intergrading cytotypes. Plants with $2n = 50$, 60 (Fig. 9), and 70 were documented; moreover, plants with $2n = 60$ and 70 were collected from the same population (voucher *Killeen 2026*, Table 1). Aposporous apomixis was reported for the species by Carman & Hatch (1982), and this reproductive scheme may explain these polyploid polymorphisms.









FIGURES 1–11. Photomicrographs of root-tip squashes.—1. *Arundinella hispida*, $2n = 20$ (*Killeen 2593*).—2. *Imperata tenuis*, $2n = 20$ (*Killeen 2482*).—3. *Lasiacis sorghoidea*, $2n = 36$ (*Killeen 2332*).—4. *Panicum laxum*, $2n = 40$ (*Killeen 2286*).—5. *Panicum olyroides*, $2n = 36$ (*Killeen 2398*).—6. *Paspalum guenoarum*, $2n = 40$ (*Killeen 2394*).—7. *Paspalum limbatum*, $2n = 20$, (*Killeen 2453*).—8. *Paspalum maculosum*, $2n = 40$ (*Killeen 2282*).—9. *Schizachyrium sanguineum*, $2n = 60$ (*Killeen 2095*).—10. *Setaria vulpiseta*, $2n = 54$, (*Killeen 2318*).—11. *Sorghastrum setosum*, $2n = 20$ (*Killeen 2306*).

Setaria vulpiseta was documented to have a chromosome number of $2n = 54$ (Fig. 10). This differs from previous reports of $2n = 36$ for Brazilian populations (de Oliveira Freitas Sacchet, 1980).

Thrasya petrosa is another species with both diploid and tetraploid cytotypes (Table 1). This combination of ploidy levels within the same species in the closely related genus *Paspalum* is usually associated with sexuality and self-incompatibility in diploids and self-fertility coupled with pseudogamous apomixis in tetraploids (Quarín & Norrmann, 1987; Norrmann et al., 1989; Quarín, 1992). A hexaploid cytotype is also known for *Th. petrosa* from Venezuela (Davidse & Pohl, 1974). It, plus the tetraploid form from the same country, showed the meiotic irregularities often associated with apomixis.

Several of the species included in this study (*Axonopus fissifolius*, *Leersia hexandra*, *Panicum laxum*, *Paspalum guenoarum*, *Paspalum lenticulare*, *Paspalum plicatulum*, *Schizachyrium sanguineum*, and *Thrasya petrosa*) have been identified as important forage species in the cerrado and pantanal savannas of central South America (Killeen, 1991a, b). Knowledge of their taxonomy and reproductive biology are essential for their improvement via breeding programs, as well as to insure the development of appropriate range management strategies.

Literature Cited

Bowden, W. M. & H. Senn. 1962. Chromosome numbers in 28 grass genera from South America. Canad. J. Bot. 40: 1115–1124.

Carman, J. G. & S. L. Hatch. 1982. Aposporous apomixis in *Schizachyrium* (Poaceae: Andropogoneae). Crop Sci. (Madison) 22: 1252–1255.

Connor, H. E. 1979. Breeding systems in the grasses: A survey. New Zealand J. Bot. 17: 131–154.

Darlington, C. D. & A. P. Wylie. 1956. Chromosome Atlas of Flowering Plants. Macmillan, New York.

Davidse, G. & R. W. Pohl. 1974. Chromosome numbers, meiotic behavior, and notes on tropical American grasses (Gramineae). Canad. J. Bot. 52: 317–328.

———, T. Hoshino & B. K. Simon. 1986. Chromosome counts of Zimbabwean grasses (Poaceae) and an analysis of polyploidy in the grass flora of Zimbabwe. S. African J. Bot. 52: 521–528.

Dubcovsky, J. & F. Zuloaga. 1991. Números cromosómicos de especies de *Panicum* (Poaceae, Paniceae). Bol. Soc. Argent. Bot. 27: 201–206.

Dujardin, M. & W. Hanna. 1984. Microsporogenesis, reproductive behavior and fertility in five *Pennisetum* species. Theor. Appl. Genet. 67: 197–201.

Fedorov, A. 1969. Chromosome Numbers of Flowering Plants. Komarov Botanical Institute of the Academy of Sciences of the U.S.S.R. [Reprinted by Koeltz Scientific Publications, Koenigstein, Germany (1974).]

Goldblatt, P. 1981. Index to Plant Chromosome Numbers, 1975–1978. Monogr. Syst. Bot. Missouri Bot. Gard. 5.

———. 1984. Index to Plant Chromosome Numbers, 1979–1981. Monogr. Syst. Bot. Missouri Bot. Gard. 8.

———. 1985. Index to Plant Chromosome Numbers, 1982–1983. Monogr. Syst. Bot. Missouri Bot. Gard. 13.

———. 1988. Index to Plant Chromosome Numbers, 1984–1985. Monogr. Syst. Bot. Missouri Bot. Gard. 23.

——— & D. E. Johnson. 1990. Index to Plant Chromosome Numbers, 1986–1987. Monogr. Syst. Bot. Missouri Bot. Gard. 30.

Gould, F. W. & T. R. Soderstrom. 1967. Chromosome numbers of tropical American grasses. Amer. J. Bot. 54: 676–683.

Honfi, A. I., C. L. Quarín & J. F. M. Valls. 1990. Estudios cariológicos en gramíneas sudamericanas. Darwiniana 30: 87–94.

Killeen, T. J. 1990. The grasses of Chiquitanía, Santa Cruz, Bolivia. Ann. Missouri Bot. Gard. 77: 125–201.

———. 1991a. Range management and land-use practices in Chiquitanía, Santa Cruz, Bolivia. Rangelands 13: 59–63.

———. 1991b. The effect of grazing on native Gramineae in Concepción, Santa Cruz, Bolivia. Trop. Grasslands 25: 12–19.

Molina, A. M. 1981. El género *Erianthus* (Gramineae) en la Argentina y países limítrofes. Darwiniana 23: 559–585.

Moore, R. J. 1973. Index to Plant Chromosome Numbers for 1967–1971. Regnum Veg. 90. Utrecht.

———. 1977. Index to Plant Chromosome Numbers for 1973–1974. Regnum Veg. 96. Utrecht.

Normann, G., C. Quarín & B. Burson. 1989. Cytogenetics and reproductive behavior of different chromosome races in six *Paspalum* species. J. Heredity 80: 24–28.

Oliveira Freitas Sacchet, A. M. de. 1980. *In:* Chromosome number reports LXIX. Taxon 29: 703–704.

Ornduff, R. 1967. Index to Plant Chromosome Numbers for 1965. Regnum Veg. 50. Utrecht.

———. 1968. Index to Plant Chromosome Numbers for 1968. Regnum Veg. 55. Utrecht.

———. 1969. Index to Plant Chromosome Numbers for 1969. Regnum Veg. 59. Utrecht.

Quarín, C. 1992. The nature of apomixis and its origin in panicoid grasses. Apomixis Newslett. 5: 8–15.

——— & G. Norrmann. 1987. Relaciones entre el número de cromosomas, su comportamiento en la meiosis y el sistema reproductivo del género *Paspalum*. *In*: Anales del IV Congreso Latinoamericano de Botánica, Bogotá, Colombia 3: 25–35.

Ramiah, K. 1935. Rice genetics. Proc. Assoc. Econ. Biol. Coimbatore 3: 51–61.

Raven, P. H. 1975. The bases of angiosperm phylogeny: Cytology. Ann. Missouri Bot. Gard. 62: 724–764.

CHROMOSOME NUMBERS AND INCIDENCE OF POLYPLOIDY IN PANICOIDEAE (POACEAE) FROM PAKISTAN[1]

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Abstract

Chromosome numbers in 126 accessions representing 58 taxa belonging to 27 genera of Panicoideae from Pakistan are reported. Chromosome numbers of three species viz. *Panicum atrosanguineum* ($n = 18$), *Pennisetum lanatum* ($n = 18$), and *Elionurus royleanus* ($n = 10$) are new determinations. New cytotypes are reported for *Isachne himalaica* (tetraploid) and *Setaria intermedia* (tetraploid). Chromosomal counts for 30 other species are new to the flora of Pakistan. More than two-thirds of the species investigated were found to be polyploid in nature.

Members of Poaceae have been of great interest from both evolutionary and cytotaxonomic points of view. The role of polyploidy in the evolution and diversification of grasses has been exceptionally large. Nearly all genera and a majority of species in this family possess chromosome numbers which are multiple of the original basic number. According to Stebbins (1950, 1956), polyploidy has played an important role in the production of a wide range of chromosome numbers in grasses. Further, he estimated nearly 70–75% of grass species to be polyploid. Sharma (1985) estimated 63.41% polyploidy in the Himalayan grasses. Baquar (1976) observed only 30.40% polyploidy among members of the family Poaceae from Pakistan. In the present study the level of polyploidy is discussed in the light of available information about the chromosome counts of Panicoideae from Pakistan.

Materials and Methods

For meiotic preparations young, unopened inflorescences were fixed in 1:3 acetic alcohol and stored at −4°C, and the anthers were squashed in 1.8% aceto-orcein. For mitotic preparations young and healthy root tips from germinating seeds were pretreated with 0.002 M 8-hydroxyquinoline for 4–6 hr., fixed in acetic alcohol (1:3) for 1 hr., hydrolysed in 1 N HCl for 6–12 min. at 60°C, and squashed in 1.8% aceto-orcein. The slides were analyzed and photographs were taken before making them permanent in euparal or Canada balsam.

Observations and Results

Table 1 lists chromosome numbers for 126 records representing 58 taxa of 27 genera. Counts new to science and new to the flora of Pakistan are specified on the basis of survey of IPCN (Fedorov, 1974; Goldblatt, 1981, 1984, 1985, 1988; Moore, 1973, 1974; Ornduff, 1967). Ploidy level was inferred from the lowest known diploid number in the genus.

Out of a total of 58 taxa investigated, 39 (67.24%) were found to be polyploid. The majority of the polyploids were at the tetraploid level. Only eight hexaploids, five octoploids and one decaploid taxa were observed.

In Table 1 the genera are arranged in tribes following Cope (1982), and the species are arranged alphabetically within genera. Voucher specimens, identified with the help of Flora of Pakistan (Cope, 1982), are deposited in Karachi University Herbarium (KUH).

Discussion

The investigated species belong to three tribes of Panicoideae. In Pakistan the tribe Isachneae is represented by a single species, *Isachne himalaica* (Fig. 19). Previously the pentaploid of this species with $2n = 50$ was reported by Mehra (1982) and Parkash (1979). The report presented here is the first of a tetraploid ($n = 20$) cytotype in this species.

The tribe Paniceae is one of the largest tribes

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TABLE 1. Chromosome numbers and ploidy level in taxa of Panicoideae (Poaceae) from Pakistan. K.U. = Karachi University. D. G. Khan = town of Dera Ghazi Khan.

Taxon	Chromosome no. *n*	Ploidy level	Voucher
Tribe Isachneae			
******Isachne himalaica* Hook. f. (Fig. 19)	20	Tetraploid	Sargodha: *Ghafoor 3848*
Tribe Paniceae			
******Brachiaria deflexa* (Schumach.) C. E. Hubbard ex Robyns (Fig. 1)	18	Tetraploid	Hazara: *Omer 2222*; Dir: *Ghafoor 2331*; D. G. Khan: *Ghafoor 3692*
******Brachiaria eruciformis* (Sm.) Stapf	9	Diploid	K.U. Campus: *Ahsan 65*; Soon Sakesar: *T. Ali 1730*
Brachiaria ramosa (L.) Stapf	18	Tetraploid	K.U. Campus: *Jahan 57*
Brachiaria ramosa (Fig. 2)	36+3B	Octoploid	K.U. Campus: *Jahan 58*
******Brachiaria reptans* (L.) Gardner & Hubbard (Fig. 3)	7	Diploid	K.U. Campus: *Ahsan 78, Moin. 48, Razaq 128*; Head Rajkan: *Ghafoor 3523*
Cenchrus biflorus Roxb. (Fig. 4)	17	Aneuploid	K.U. Campus: *Ahsan 44*
Cenchrus biflorus	16	Aneuploid	Mianwali: *T. Ali 1811*
******Cenchrus ciliaris* L.	18	Diploid	Layyah: *Ghafoor 3747*; D. G. Khan: *Ghafoor 3625*
Cenchrus ciliaris	17	Aneuploid	K.U. Campus: *Razaq 133*; Makran: *T. Ali 835*; Attock: *Ghafoor 2268*
Cenchrus pennisetiformis Hochst. & Steud. ex Steud.	18	Diploid	K.U. Campus: *Siddiqui 2*
Cenchrus setigerus Vahl	17	Aneuploid	Safari Park, Karachi: *Siddiqui 63*; D. G. Khan: *Ghafoor 3603*; Mianwali: *T. Ali 1824*; Darsanochano: *Siddiqui 88*; K.U. Campus: *Siddiqui 50*; Kathore: *Jahan 66, 78*; Manghopir: *Razaq 159*
******Digitaria ciliaris* (Retz.) Koeler	27	Hexaploid	K.U. Campus: *Siddiqui 32*; *Razaq 146*
Digitaria ciliaris	36	Octoploid	Kashmir: *T. Ali 20*
******Digitaria nodosa* Parl. (Fig. 5)	9	Diploid	K.U. Campus: *Moin. 68*
******Digitaria setigera* Roth ex Roem. & Schult.	36	Octoploid	Hazara: *Omer 2739*
******Digitaria stricta* Roth ex Roem. & Schult.	18	Tetraploid	Pail: *Ghafoor 3791*
Echinochloa colona (L.) Link	9	Diploid	Dir: *Ghafoor 4093*
Echinochloa colona	18	Tetraploid	K.U. Campus: *Jahan 20*
Echinochloa colona	27	Hexaploid	Kashmir: *T. Ali 400*; Makran: *T. Ali 836*; Zhob: *T. Ali 1087*; K.U. Campus: *Ahsan 7*; Baltistan: *Omer 2539*
******Echinochloa crus-galli* (L.) P. Beauv.	27	Hexaploid	Kashmir: *T. Ali 46*
Echinochloa crus-galli (Fig. 20)	45	Decaploid	Thatta: *Siddiqui 153*
******Echinochloa frumentacea* Link	27	Hexaploid	Khushab: *Ghafoor 3796*
******Eriochloa fatmensis* (Hochst. & Steud.) W. D. Clayton	9	Diploid	K.U. Campus: *Moin. 52*
Eriochloa fatmensis	18	Tetraploid	K.U. Campus: *Ahsan 53*
******Eriochloa procera* (Retz.) C. E. Hubbard	9	Diploid	K.U. Campus: *Moin. 49, 50*
Eriochloa procera	18	Tetraploid	Sajawal: *Ahsan 21*; Thatta: *Siddiqui 121*
Panicum antidotale Retz.	9	Diploid	K.U. Campus: *Razaq 123*
*******Panicum atrosanguineum* Hochst. ex A. Rich. (Fig. 6)	18	Tetraploid	Khushab: *Ghafoor 3823*
******Panicum maximum* Jacq. (Fig. 7)	9	Diploid	Hasilpur: *Ghafoor 3584*; Mianwali: *T. Ali 1816*
******Panicum miliaceum* L.	18	Tetraploid	Bahawalpur: *Ghafoor 3528*
******Panicum repens* L. (Fig. 8)	9	Diploid	Makran: *Omer 2165*

TABLE 1. Continued.

Taxon	Chromosome no. *n*	Ploidy level	Voucher
**Panicum turgidum* Forssk.	9	Diploid	Makran: *T. Ali 855*; K.U. Campus: *Siddiqui 41*; * Kashmir: *T. Ali 128*
**Paspalidium flavidum* (Retz.) A. Camus	27	Hexaploid	Rawalpindi: *Ghafoor 4152*
Paspalidium geminatum (Forssk.) Stapf (Fig. 9)	9	Diploid	K.U. Campus: *Moin. 69, 59*
**Paspalum dilatatum* Poir.	30	Hexaploid	Gilgit: *Omer 2591, 2271*; Rawalpindi: *Ghafoor 4176*
**Paspalum paspalodes* (Michx.) Scribner (Fig. 10)	30	Hexaploid	K.U. Campus: *Jahan 40, 41*; Swat: *Ghafoor 3334*; Sukkur: *Ghafoor 3492*; Thatta: *Siddiqui 132*
**Pennisetum flaccidum* Griseb.	27	Hexaploid	Dir: *Ghafoor 2408*
**Pennisetum glaucum* (L.) R. Br.	7	Diploid	K.U. Campus: *Moin. 73*
***Pennisetum lanatum* Klotzsch (Fig. 11)	18	Tetraploid	Swat: *Ghafoor 3429*
**Pennisetum orientale* Rich.	9	Diploid	Soon Sakesar: *T. Ali 1624*
Pennisetum orientale (Fig. 12)	18	Tetraploid	Makran: *T. Ali 1006*
Setaria intermedia Roem. & Schult. (Fig. 21)	18	Tetraploid	K.U. Campus: *Ahsan 76*
**Setaria pumila* (Poir.) Roem. & Schult.	36	Octoploid	Vehari: *Ghafoor 3598*; Chitral: *Ghafoor 2493*
**Setaria verticillata* (L.) P. Beauv.	9	Diploid	K.U. Campus: *Moin. 70*; Safari Park, Karachi: *Siddiqui 72*
Tribe Andropogoneae			
Apluda mutica L.	10	Diploid	D. G. Khan: *Ghafoor 3711*
**Arthraxon lancifolius* (Trin.) Hochst.	9	Diploid	Kashmir: *T. Ali 194*
Arthraxon prionodes (Steud.) Dandy (Fig. 14)	18	Tetraploid	Soon Sakesar: *T. Ali 1724, 1701*
Arthraxon prionodes (Fig. 13)	10	Aneuploid	Hazara: *Omer 2265*
Bothriochloa ischaemum (L.) Keng	20	Tetraploid	Gilgit: *Omer 2617*; Chitral: *Ghafoor 3218*
Capillipedium parviflorum (R. Br.) Stapf	20	Tetraploid	Kashmir: *T. Ali 266*
Chrysopogon aucheri (Boiss.) Stapf	10	Diploid	K.U. Campus: *Moin. 1*; Safari Park, Karachi: *Siddiqui 67*; Kathore: *Jahan 86*; Makran, *T. Ali 830*
Chrysopogon gryllus (L.) Trin. subsp. *echinulatus* (Nees) T. A. Cope	10	Diploid	Swat: *Ghafoor 3431*
Chrysopogon serrulatus Trin. (Fig. 15)	10	Diploid	Hazara: *Omer 2267*
Cymbopogon jwarancusa (Jones) Schult.	20	Tetraploid	Safari Park, Karachi: *Siddiqui 73*; K.U. Campus: *Jahan 55*; Choa Sayyadan Shah: *T. Ali 1872*
**Cymbopogon martinii* (Roxb.) W. Watson	20	Tetraploid	Kashmir, *T. Ali 207*
Dichanthium annulatum (Forssk.) Stapf	20	Tetraploid	Kashmir: *T. Ali 14*; Attock: *Ghafoor 2275*; *Ghafoor 2276*; K.U. Campus: *Moin. 4, Jahan 54*
Dichanthium foveolatum (Delile) Roberty (Fig. 16)	20	Tetraploid	K.U. Campus: *Ahsan 57*; Kasmir: *T. Ali 35*; Attock: *Ghafoor 4232*
***Elionurus royleanus* Nees ex A. Rich. (Fig. 17)	10	Tetraploid	K.U. Campus: *Moin. 65*
**Hackelochloa granularis* (L.) Kuntze	7	Diploid	K.U. Campus: *Ahsan 30*

TABLE 1. Continued.

Taxon	Chromosome no. *n*	Ploidy level	Voucher
Heteropogon contortus (L.) P. Beauv. ex Roem. & Schult. (Fig. 22)	10	Diploid	Pail: *Ghafoor 3858*; K.U. Campus: *Moin. 38*
Heteropogon contortus	20	Tetraploid	Kashmir: *T. Ali 32*
Lasiurus scindicus Henr.	9	Diploid	Cholistan: *Ghafoor 3545*; Makran: *T. Ali 829*; *Omer 2117*; K.U. Campus: *Razaq 167*, *Siddiqui 46*
Phacelurus speciosus (Steud.) C. E. Hubbard	10	Diploid	Chitral: *Ghafoor 2705*
Saccharum griffithii Munro ex Boiss. (Fig. 23)	10	Diploid	D. G. Khan: *Ghafoor 3616*
Saccharum spontaneum L. (Fig. 24)	27	Aneuploid	Sargodha: *T. Ali 1667*
**Sorghum bicolor* (L.) (Fig. 18)	10	Tetraploid	Makran: *Omer 2043*
Sorghum halepense (L.) Pers.	20	Octoploid	Chitral: *Ghafoor 3215*; Muzaffargarh: *Ghafoor 3757*; Chakwal: *Ghafoor 4247*; K.U. Campus: *Jahan 38*
Vetiveria zizanioides (L.) Nash	10	Diploid	Sialkot: *Ghafoor 4310*
**Zea mays* L.	$2n = 20$	Diploid	Darsanochano: *Siddiqui 94*

* Count new to flora of Pakistan.
** Count new to science.

of the grass family. In Pakistan it is represented by 15 genera and 73 species (Cope, 1982). Species of 11 of these genera were studied. *Brachiaria reptans* with $n = 7$ (Fig. 3) and *B. eruciformis* with $n = 9$ are diploids based on $x = 7$ and 9 respectively. These counts are new to the flora of Pakistan and conform with earlier counts reported from other regions (Malik & Mary, 1970; Christopher & Abraham, 1976; Basappa & Muniyamma, 1981; Mehra, 1982). *Brachiaria deflexa*, with $n = 18$ (Fig. 1), is tetraploid on the basis of $x = 9$. In *B. ramosa* we observed three B-chromosomes in addition to 36 bivalents.

Both $n = 17$ and $n = 18$ are recorded in the genus *Cenchrus*. As far as the basic number is considered, Löve and Löve (1961) regarded $x = 17$ as the basic number, while Baquar and Anjum (1969) regarded $x = 9$ as the basic number. Though $n = 9$ is found in other genera of the tribe, $n = 9$ is hitherto unknown in the genus *Cenchrus*. Therefore, in our opinion, the basic number for this genus is $x = 18$, reflecting an early tetraploid origin, and $x = 17$ is an aneuploid descendant from $x = 18$.

A new chromosome count for *Panicum atrosanguineum* ($n = 18$, Fig. 6) revealed that it is a tetraploid species.

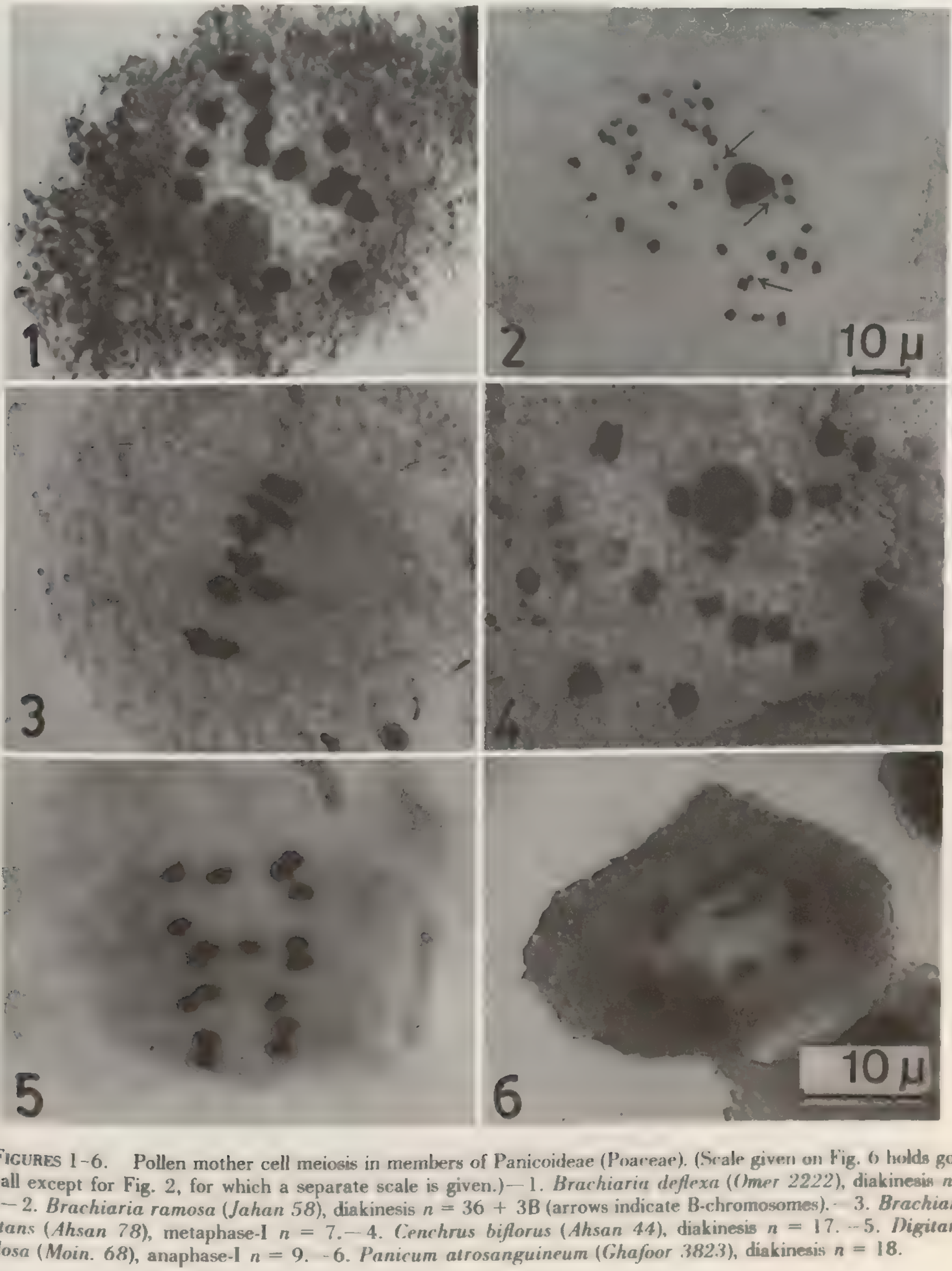
Pennisetum is agronomically an important genus, with $n = 7$ and $n = 9$. *Pennisetum lanatum* (Fig. 11) has been reported for the first time to be tetraploid ($n = 18$).

The base number for the genus *Setaria* is $x = 9$. In the present study three species, namely, *S. intermedia* ($n = 18$; Fig. 21), *S. pumila* ($n = 36$), and *S. verticillata* ($n = 9$) show great cytological variability. Baquar and Saeed (1969) reported $n = 9$, while Raman et al. (1959) reported $n = 27$ for *S. intermedia*, but we are reporting a new ploidy level, i.e., $n = 18$, for the same species.

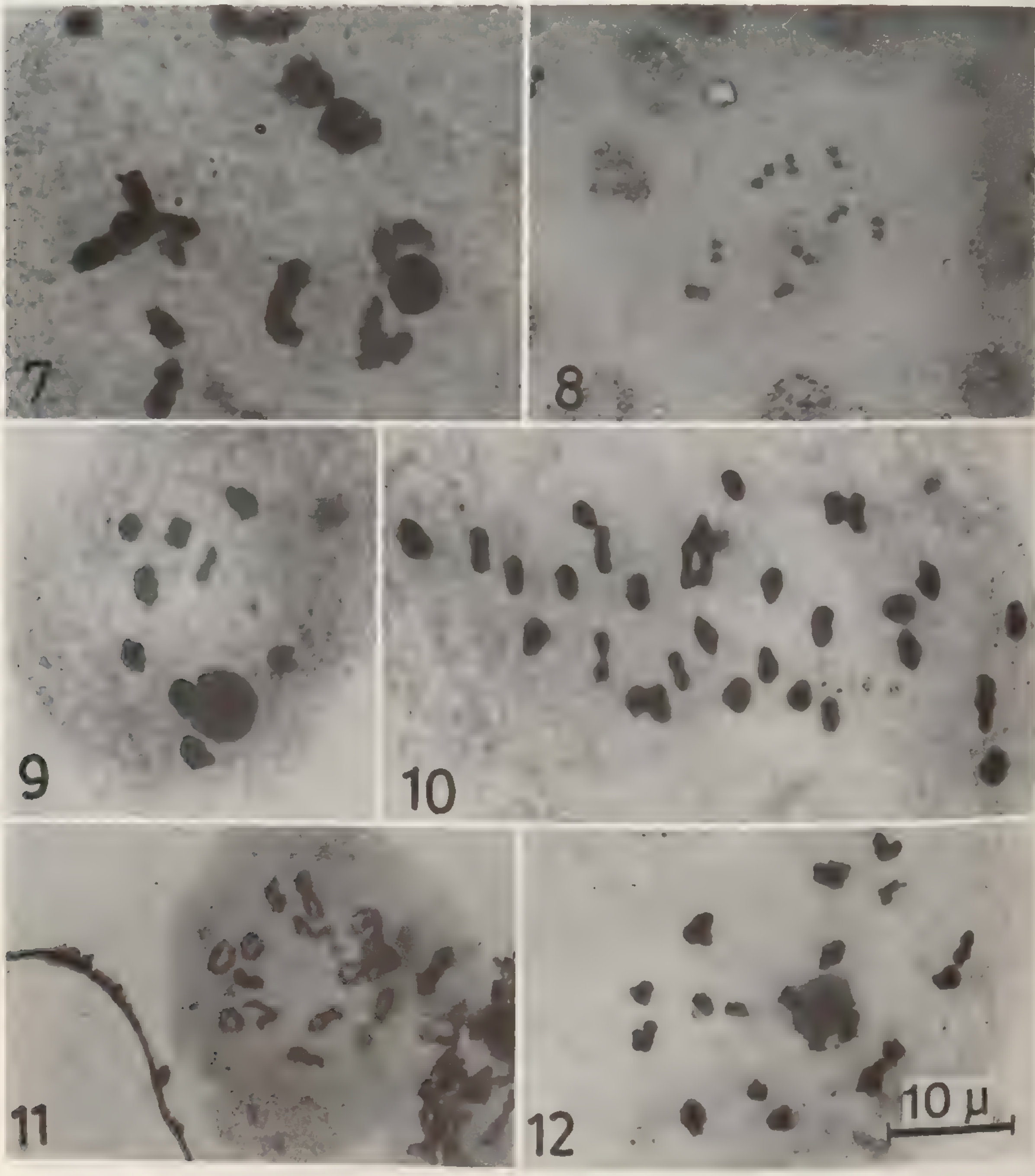
In Pakistan the tribe Andropogoneae is represented by 36 genera and 67 species (Cope, 1982). In the present study, species belonging to 17 genera of the tribe have been investigated cytologically. In *Arthraxon prionodes*, $n = 10$ (Fig. 13) and $n = 18$ (Fig. 14) are reported here, numbers which may be hyperaneuploid and tetraploid with respect to the basic number, $x = 9$.

The chromosome count for *Elionurus royleanus* (Fig. 17) is reported here for the first time. We believe that it is a tetraploid species ($n = 10$). This is substantiated by the report (Dujardin, 1978) that *E. hesii* has $n = 5$.

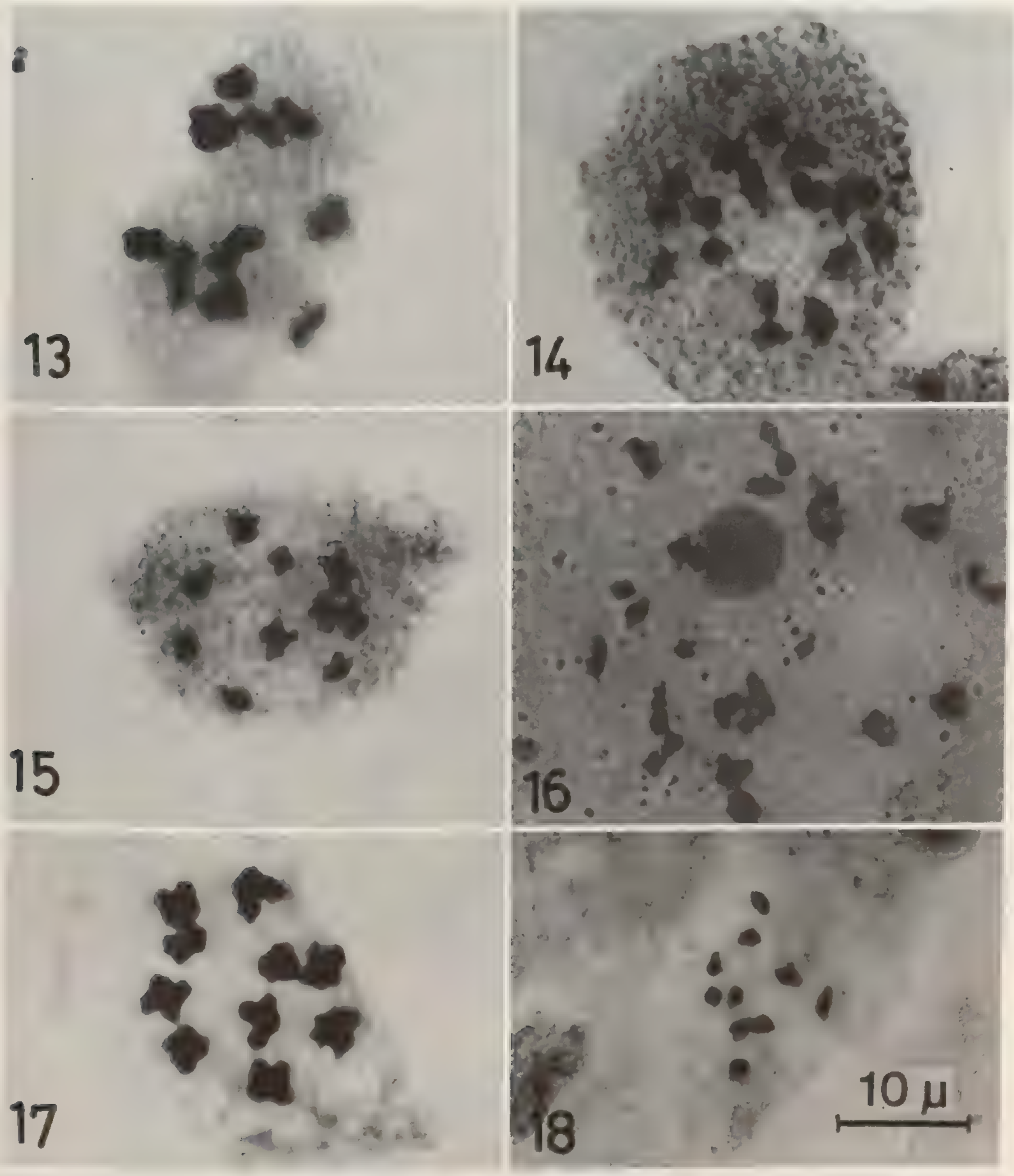
The basic number for the genus *Lasiurus* is $x = 9$. The present and previous reports (Faruqi et al., 1979) both indicate the presence of only diploid populations in Pakistan, whereas the count given



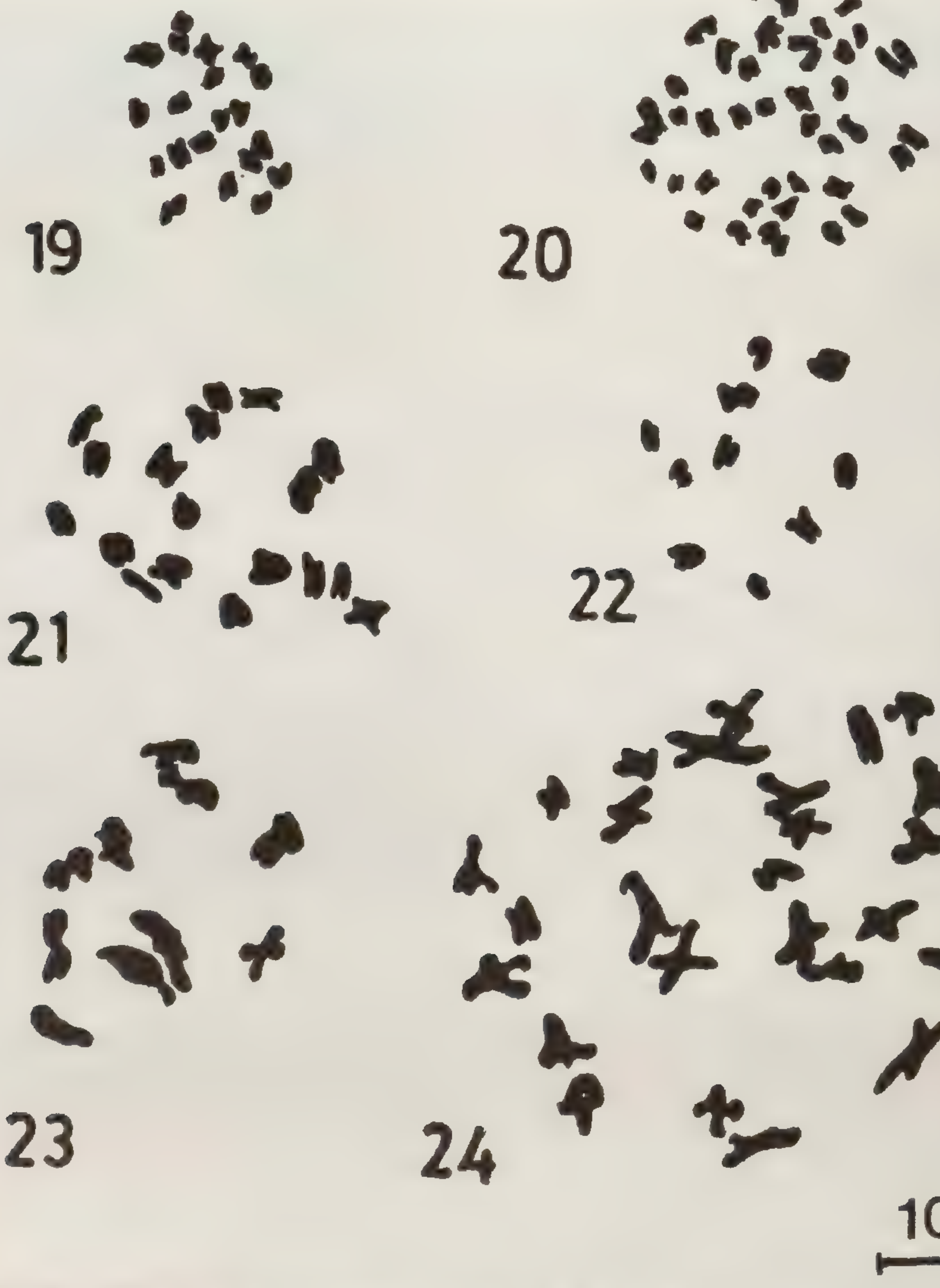
FIGURES 1–6. Pollen mother cell meiosis in members of Panicoideae (Poaceae). (Scale given on Fig. 6 holds good for all except for Fig. 2, for which a separate scale is given.)—1. *Brachiaria deflexa* (*Omer 2222*), diakinesis $n = 18$.—2. *Brachiaria ramosa* (*Jahan 58*), diakinesis $n = 36 + 3B$ (arrows indicate B-chromosomes).—3. *Brachiaria reptans* (*Ahsan 78*), metaphase-I $n = 7$.—4. *Cenchrus biflorus* (*Ahsan 44*), diakinesis $n = 17$.—5. *Digitaria nodosa* (*Moin. 68*), anaphase-I $n = 9$.—6. *Panicum atrosanguineum* (*Ghafoor 3823*), diakinesis $n = 18$.



FIGURES 7–12. Pollen mother cell meiosis in members of Panicoideae (Poaceae). —7. *Panicum maximum* (*Ghafoor 3584*), diakinesis $n = 9$. —8. *Panicum repens* (*Omer 2165*), diakinesis $n = 9$. —9. *Paspalidium geminatum* (*Moin. 69*), diakinesis $n = 9$. —10. *Paspalum paspalodes* (*Jahan 40*), metaphase-I $n = 30$. —11. *Pennisetum lanatum* (*Ghafoor 3429*), diakinesis $n = 18$. —12. *Pennisetum orientale* (*T. Ali 1006*), diakinesis $n = 18$.



FIGURES 13–18. **Pollen mother cell meiosis in members of Panicoideae (Poaceae).** — 13. *Arthraxon prionodes* (*Omer 2265*), metaphase-I $n = 10$.—14. *Arthraxon prionodes* (*T. Ali 1724*), diakinesis $n = 18$.—15. *Chrysopogon serrulatus* (*Omer 2267*), diakinesis $n = 10$.—16. *Dichanthium foveolatum* (*Ahsan 57*), diakinesis $n = 20$.—17. *Elionurus royleanus* (*Moin. 65*), metaphase-I $n = 10$. —18. *Sorghum bicolor* (*Omer 2043*), metaphase-I $n = 10$.



FIGURES 19–24. Pollen mother cell meiosis in members of Panicoideae (Poaceae).—19. *Isachne himalaica* (*Ghafoor 3848*), metaphase-I $n = 20$.—20. *Echinochloa crus-galli* (*Siddiqui 153*), diakinesis $n = 45$.—21. *Setaria intermedia* (*Ahsan 76*), diakinesis $n = 18$.—22. *Heteropogon contortus* (*Ghafoor 3858*), diakinesis $n = 10$.—23. *Saccharum griffithii* (*Ghafoor 3616*), diakinesis $n = 10$.—24. *Saccharum spontaneum* (*T. Ali 1667*), diakinesis $n = 27$.

by Celarier (1957) indicates the presence of aneuploidy at hexaploid level.

The present investigation of polyploidy in Panicoideae from Pakistan demonstrates a prevalence of eupolyploidy as well as aneuploidy. From the total of 58 taxa cytologically studied, only 26 were diploids while the rest of the species were either aneuploids or eupolyploids. The common ploidy levels were tetraploid and hexaploid, though, rarely, octoploid and decaploid levels were also observed.

LITERATURE CITED

BAQUAR, S. R. 1976. Polyploidy in the Flora of Pakistan in relation to latitude, life form and taxonomic groups. Taxon 25: 621–627.

——— & V. ANJUM. 1969. Chromosome behaviour in *Cenchrus* complex from southern West Pakistan. Portugaliae Acta Biologica XI(3–4): 288–296.

——— & M. SAEED. 1969. Chromosome studies and polyploid analysis in grasses of West Pakistan I. Caryologia 22: 103 112.

BASAPPA, G. P. & M. MUNIYAMMA. 1981. Chromosome Number Reports LXXII. Taxon 30: 703.

CELARIER, R. P. 1957. Cytotaxonomy of the Andro-

pogoneae. II. Subtribes Ischaemineae, Rottboelliinae, and the Maydeae. Cytologia 22: 160 183.

CHRISTOPHER, J. & A. ABRAHAM. 1976. Studies on the cytology and phylogeny of south Indian grasses. III. Subfamily VI: Panicoideae, tribe Paniceae. Cytologia 41: 621–637.

COPE, T. A. 1982. Poaceae. *In:* E. Nasir & S. I. Ali (editors), Flora of West Pakistan 143: 1–678.

DUJARDIN, M. 1978. Chromosome numbers of some tropical African grasses from Western Zaire. Canad. J. Bot. 56: 2138–2152.

FARUQI, S. A., H. B. QURAISH & N. HALAI. 1979. Chromosome numbers and some morphological characteristics of some Andropogoneae from Pakistan. Cytologia 44: 585–605.

FEDOROV, A. A. (editor). 1974. Chromosome Numbers of Flowering Plants. Otto Koeltz Science Publishers, West Germany (reprinted).

GOLDBLATT, P. (editor). 1981. Index to Plant Chromosome Numbers 1975–1978. Monogr. Syst. Bot. Missouri Bot. Gard. 5: 1–553.

———. 1984. Index to Plant Chromosome Numbers 1979–1981. Monogr. Syst. Bot. Missouri Bot. Gard. 8: 1–427.

———. 1985. Index to Plant Chromosome Numbers 1982–1983. Monogr. Syst. Bot. Missouri Bot. Gard. 13: 1–224.

———. 1988. Index to Plant Chromosome Numbers 1984–1985. Monogr. Syst. Bot. Missouri Bot. Gard. 23: 1–264.

LÖVE, A. & D. LÖVE. 1961. Chromosome numbers of Central and Northwest European plant species. Opera Botanica 5: 1–581.

MALIK, C. P. & T. N. MARY. 1970. Chromosome Number Reports XXVII. Taxon 19: 437–442.

MEHRA, P. N. 1982. Cytology of East Indian Grasses. P. N. Mehra, Chandigarh.

MOORE, R. J. (editor). 1973. Index to Plant Chromosome Numbers for 1967–1971. Regnum Vegetabile 90: 1–539.

———. 1974. Index to Plant Chromosome Numbers for 1972. Regnum Vegetabile 91: 1–108.

ORNDUFF, R. (editor). 1967. Index to Plant Chromosome Numbers for 1965. Regnum Vegetabile 50: 1–128.

PARKASH, O. 1979. Cytological Investigations in Some Grasses of Northeastern India (Festucoids, *Ischaemum* Linn., *Eulalia* Kunth and *Saccharum spontaneum* Linn.). Ph.D. Thesis, Chandigarh.

RAMAN, V. S., P. CHANDRASEKHARAN & D. KRISHNASWAMI. 1959. Chromosome numbers in Gramineae. Curr. Sci. 28: 453–454.

SHARMA, M. L. 1985. Climato-geographic polyploidy variations in the Himalayan Grasses. Cytologia 50: 483–486.

STEBBINS, G. L. 1950. Variation and Evolution in Plants. Columbia Univ. Press, New York.

———. 1956. Cytogenetics and evolution of the grass family. Amer. J. Bot. 43: 890–905.

CHROMOSOME COUNTS IN ARUNDINOIDEAE, CHLORIDOIDEAE, AND POOIDEAE (POACEAE) FROM PAKISTAN[1]

M. Moinuddin,[2] Ahsan A. Vahidy,[3] and S. I. Ali[2]

ABSTRACT

A total of 85 chromosome counts representing 45 species belonging to 29 genera in three subfamilies of Poaceae, viz., Arundinoideae, Chloridoideae, and Pooideae from Pakistan, are reported. The chromosome counts for six species, viz.: *Leptothrium senegalense* ($n = 10$); *Piptatherum gracile* ($n = 12$); *Poa sinaica* ($n = 7$); *Sporobolus arabicus* ($n = 18$); *Sporobolus nervosus* ($n = 18$); and *Stipagrostis plumosa* ($n = 22$), are new determinations. Chromosome counts for an additional 34 species are new for the flora of Pakistan. New cytotypes were detected in *Aeluropus lagopoides* ($n = 20$), *Avena barbata* ($n = 21$), *Diplachne fusca* ($n = 20$), and *Ochthochloa compressa* ($n = 10$).

The Poaceae are one of the largest families of flowering plants, comprising 620 genera and 10,000 species. Its members are widely dispersed in all regions of the world, occupying almost every type of habitat, often dominating the vegetation in savannas, prairies and steppes (Willis, 1973). In Pakistan, the family is represented by 158 genera and 492 species (Cope, 1982). Up to now chromosome numbers are known for 39 species (i.e., 7.92%) from Pakistan (Baquar & Anjum, 1969; Baquar & Saeed, 1969; Faruqi et al., 1979). The present contribution records the chromosome numbers of 45 species belonging to 29 genera in three subfamilies.

MATERIALS AND METHODS

For meiotic counts, young unopened inflorescences were fixed in Carnoy's solution (3 parts absolute alcohol: 1 part glacial acetic acid) for at least 24 hr., then stored at −4°C. Slides were prepared by ordinary squash technique using 1.0% acetocarmine or 1.8% aceto-orcein.

For mitotic counts, young and healthy root tips from germinating seeds were pretreated either with 0.002 M 8-hydroxyquinoline (for 4–6 hr.) or with cold water (at 1–2°C for 24 hr.), fixed in Carnoy's solution for 1 hr., hydrolysed in 1 N HCl for 6–12 min. at 60°C, and squashed in 1.8% aceto-orcein.

In most of the cases photomicrographs were taken from temporary preparations. Desired slides were made permanent in euparal or Canada balsam. Voucher specimens are deposited in Karachi University Herbarium (KUH).

OBSERVATIONS AND RESULTS

Information regarding the counts made, along with the basic number for the genus, are presented in Table 1. Basic numbers of genera were calculated from the lowest known gametic number in the genus. Chromosome numbers for six species are new to science and counts for thirty-four species are new to the flora of Pakistan, as they were not found to be reported in IPCN (Fedorov, 1974; Goldblatt, 1981, 1984, 1985, 1988; Moore, 1973, 1974).

DISCUSSION

In the present study most of the chromosome counts that are in conformity with earlier reports have not been commented upon.

In the tribe Aristideae, counts for *Stipagrostis plumosa* ($n = 22$, Fig. 1) are reported here for the first time.

In the tribe Aeluropodeae, *Aeluropus lagopoides* ($n = 20$, Fig. 20) is found to be tetraploid on the basis of $x = 10$. Diploid and pentaploid

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FIGURES 1–6. Pollen mother cell meiosis in members of Poaceae.—1. *Stipagrostis plumosa* (*Ghafoor 2776*), metaphase-I $n = 22$.—2. *Diplachne fusca* (*Siddiqui 101*), diakinesis $n = 20$.—3. *Ochthochloa compressa* (*T. Ali 752*), diakinesis $n = 10$.—4. *Sporobolus arabicus* (*T. Ali 842*), metaphase-I $n = 18$.—5. *Sporobolus nervosus* (*Siddiqui 131*), diakinesis $n = 18$.—6. *Leptothrium senegalens* (*Ahsan 68*), diakinesis $n = 10$.

individuals have previously been reported for this species (Sindhe, 1980; Baquar & Saeed, 1969).

In tribe Eragrostideae, chromosome numbers for ten species (belonging to 6 genera) were determined. In *Dactyloctenium aegyptium*, we found $n = 20$ in two and $n = 23$ in one accession. On the basis of proposed basic numbers ($x = 10, 12$) it can be suggested that individuals with $n = 20$ were tetraploid, whereas $n = 23$ represents a hypoaneuploid based on $x = 12$. Our observations ($n = 10, 20$), in two different specimens of *D. scindicum*, indicate the presence of cytotypes in this species.

Larsen (1963) had reported $2n = 20$ ($2x$) for

TABLE 1. Chromosome numbers in Poaceae from Pakistan. K.U. = Karachi University. D. G. Khan = town of Dera Ghazi Khan.

Taxon	Chromosome number *n*	Basic number *x*	Voucher
Subfamily Arundinoideae			
Tribe Arundineae			
**Schismus barbatus* (L.) Thell. (Fig. 13)	6	6	Chitral: *Ghafoor 2693, 3071*; Makran: *T. Ali 834*
Subfamily Chloridoideae			
Tribe Aristideae			
**Aristida adscensionis* L.	11	11	Makran: *T. Ali 945*
**Aristida funiculata* Trin. & Rupr. (Fig. 19)	11		K.U. Campus: *Siddiqui 4*
***Stipagrostis plumosa* (L.) Munro ex T. Anderson (Fig. 1)	22	22	Chitral: *Ghafoor 2776*
Tribe Aeluropodeae			
Aeluropus lagopoides (L.) Trin. ex Thwaites (Fig. 20)	20	10	Thatta: *Siddiqui 150, 119*; K.U. Campus: *Moin. 71*
Tribe Eragrostideae			
Dactyloctenium aegyptium (L.) Willd.	23	10, 12	K.U. Campus: *Razaq 126*
	20		K.U. Campus: *Moin. 46*; Layyah: *Ghafoor 3744*
**Dactyloctenium scindicum* Boiss.	10		K.U. Campus: *Moin. 72*
Dactyloctenium scindicum	20		K.U. Campus: *Ahsan 56*
**Dinebra retroflexa* (Vahl) Panzer	10	10	Khushab: *Ghafoor 3836*
**Diplachne fusca* (L.) P. Beauv. ex Roem & Schult. (Fig. 2)	20	10	Thatta: *Siddiqui 101*
Eleusine indica (L.) Gaertn.	9	9	K.U. Campus: *Ahsan 6*; Swat: *Ghafoor 3977*; Islamabad: *Ghafoor 3469a*
Eleusine indica	18		Makran: *Omer 2112*
**Eragrostis cilianensis* (All.) Lutati ex F. T. Hubbard	10	10	K.U. Campus: *Moin. 42*
**Eragrostis japonica* (Thunb.) Trin.	10		Lahore: *Ghafoor 4358*
**Eragrostis minor* Host	10		Hasilpur: *Ghafoor 3583*
Eragrostis minor	20		Sargodha: *T. Ali 1719*
Eragrostis pilosa (L.) P. Beauv.	20		Sakesar: *T. Ali 1605*
**Ochthochloa compressa* (Forssk.) Hilu (Fig. 3)	10	10	Makran: *T. Ali 752*
Ochthochloa compressa	20		Makran: *Omer 2166, T. Ali 710*; Safari Park, Karachi: *Ahsan 38*; K.U. Campus: *Razaq 144*; D. G. Khan: *Ghafoor 3608*
Tribe Chlorideae			
Chloris barbata Sw.	20	10	K.U. Campus: *Siddiqui 11*; Sajawal: *Ahsan 26*
**Cynodon dactylon* (L.) Pers. (Fig. 14)	9	9	K.U. Campus: *Siddiqui 31, 76, 90, Moin. 12*; Dir: *Ghafoor 2491*
**Tetrapogon tenellus* (Koen. ex Roxb.) Chiov. (Fig. 21)	10	10	K.U. Campus: *Moin. 53*
**Tetrapogon villosus* Desf.	10		D. G. Khan: *Ghafoor 3699*; Makran: *T. Ali 969*

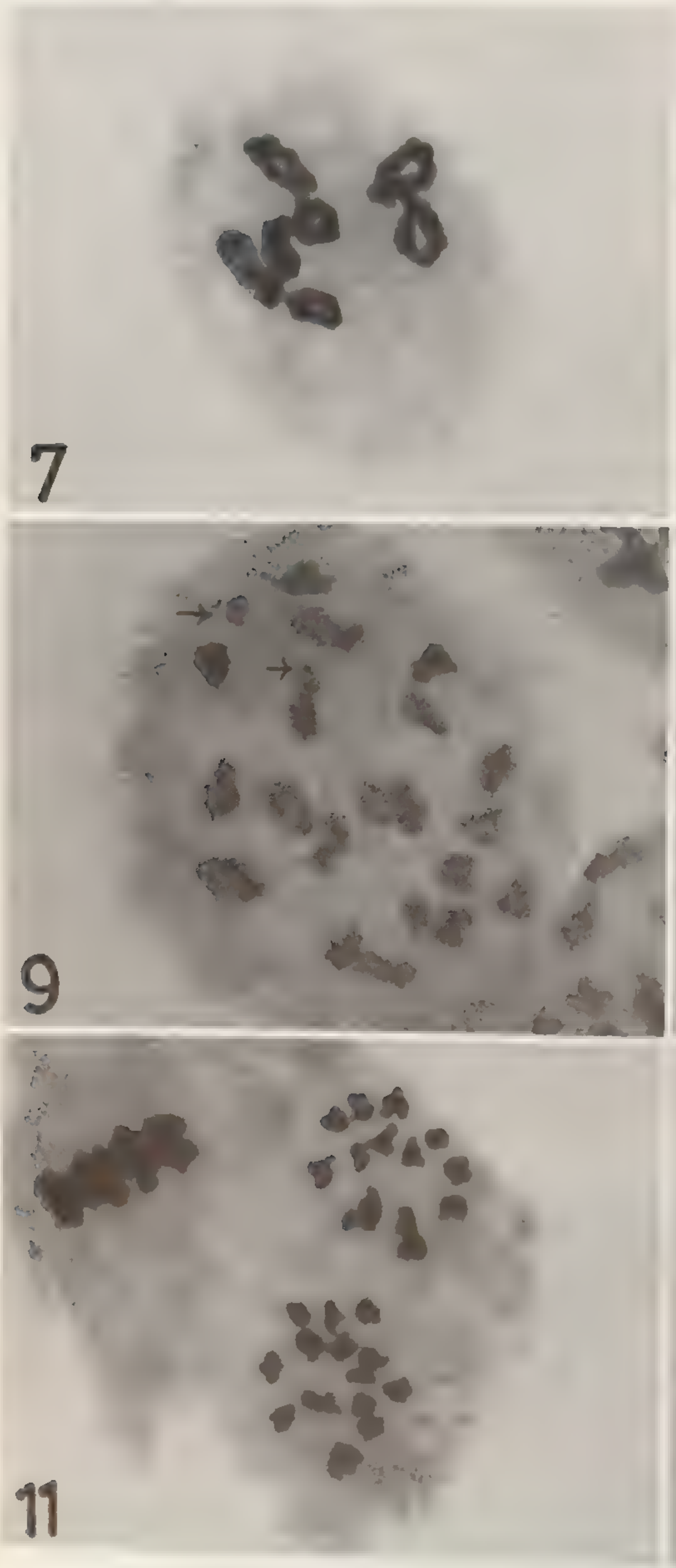
TABLE 1. Continued.

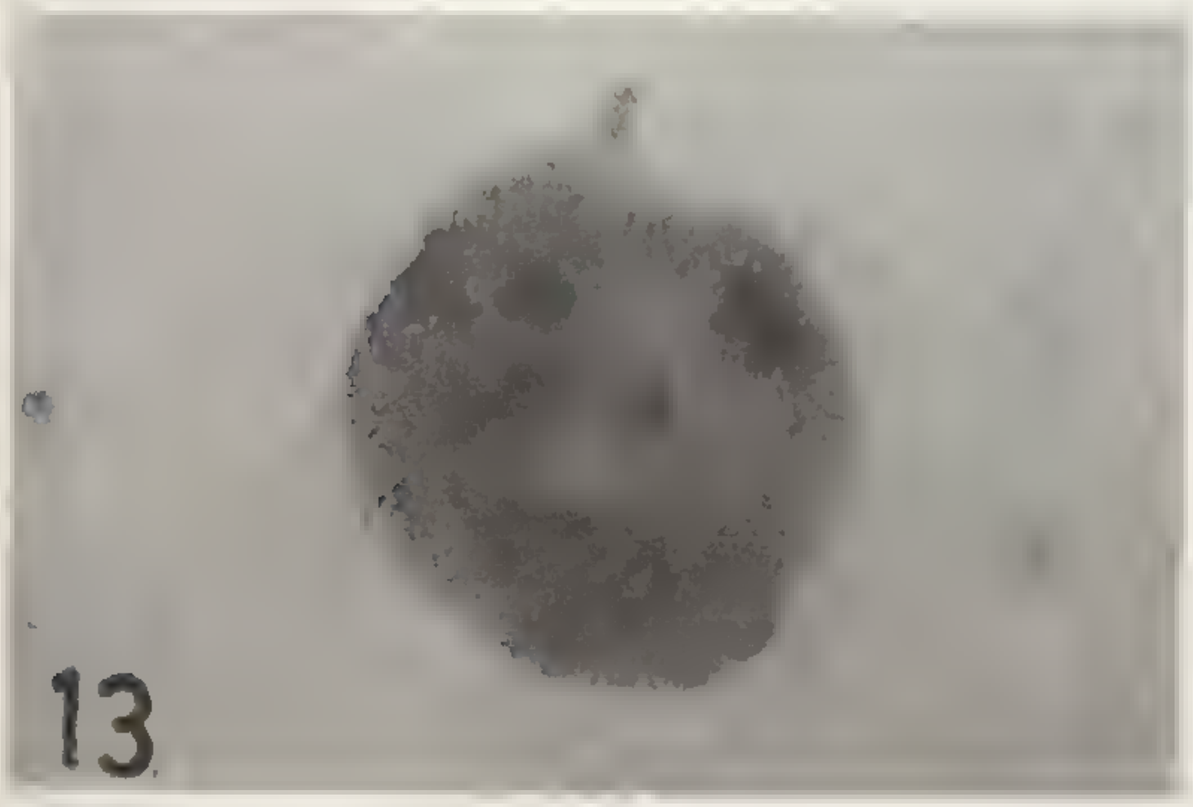
Taxon	Chromosome number *n*	Basic number *x*	Voucher
Tribe Sporoboleae			
****Sporobolus arabicus* Boiss. (Fig. 4)	18	9	Makran: *T. Ali 842, 846*; Cholistan: *Ghafoor 3550*
***Sporobolus coromandelianus* (Retz.) Kunth	18		K.U. Campus: *Moin. 56*
***Sporobolus diander* (Retz.) P. Beauv.	18		Pail: *Ghafoor 3776*
****Sporobolus nervosus* Hochst. (Fig. 5)	18		Thatta: *Siddiqui 131*; Darsanochano: *Siddiqui 80*
Tribe Zoysieae			
****Leptothrium senegalense* (Kunth) W. D. Clayton (Fig. 6)	10	10	K.U. Campus: *Ahsan 68*
***Tragus berteronianus* Schult.	10	10	Hazara: *Omer 2221*; Mianwali; *T. Ali 1856*
***Tragus roxburghii* Panigrahi	10		K.U. Campus: *Moin. 55*
Subfamily Pooideae			
Tribe Poeae			
***Dactylis glomerata* L.	7	7	Chitral: *Ghafoor 2450, 3286*
Dactylis glomerata	14		Dir: *Ghafoor 2421*
***Lolium rigidum* Gaudin (Fig. 7)	7	7	Chitral: *Ghafoor 3274*
***Poa annua* L.	14	7	Chitral: *Ghafoor 2430*; Kashmir: *T. Ali 573*; Kalam: *Ghafoor 3422*
****Poa sinaica* Steud. (Fig. 8)	7		Hazara: *Omer 2720*
Tribe Glycerieae			
***Glyceria plicata* (Fries) Fries	20	5	Chitral: *Ghafoor 2850*
Tribe Aveneae			
***Agrostis munroana* Aitch. & Hemsl. (Fig. 22)	21	7	Hazara: *Omer 2778*
***Agrostis viridis* Gouan (Fig. 9)	21+2B		Dir: *Ghafoor 2337*
Agrostis viridis	14		Chitral: *Ghafoor 2698, 2513, 3325, 2608*
***Alopecurus arundinaceus* Poir.	14	7	Hazara: *Omer 2722*
***Avena barbata* Pott ex Link (Fig. 23)	21	7	Gilgit: *Omer 2559*
***Phalaris minor* Retz. (Fig. 10)	14	7	K.U. Campus: *Jahan 19*
***Polypogon monspeliensis* (L.) Desf. (Fig. 11)	14	7	Chitral: *Ghafoor 2598, 3249*; K.U. Campus: *Siddiqui 34*; Makran: *Omer 2143*
Tribe Stipeae			
****Piptatherum gracile* Mez (Fig. 12)	12	12	Chitral: *Ghafoor 3093*
***Piptatherum munroi* (Stapf) Mez	12		Gilgit: *Omer 2464*; Swat: *Ghafoor 3412*; Dir: *Ghafoor 2407*
Tribe Bromeae			
***Bromus danthoniae* Trin. (Fig. 15)	7	7	Chitral: *Ghafoor 2916*
***Bromus pectinatus* Thunb.	7		Gilgit: *Omer 2426*
***Bromus tectorum* L. (Fig. 16)	7		Chitral: *Ghafoor 2606*

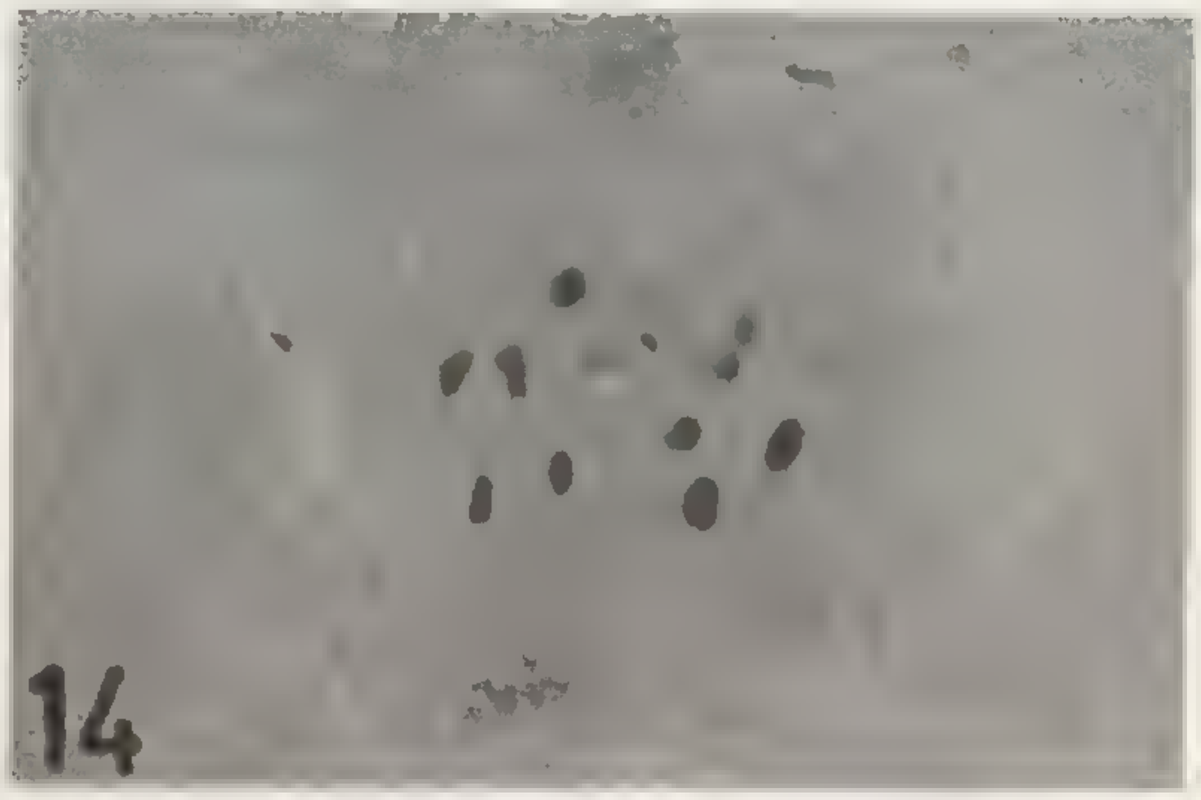
TABLE 1. Continued.

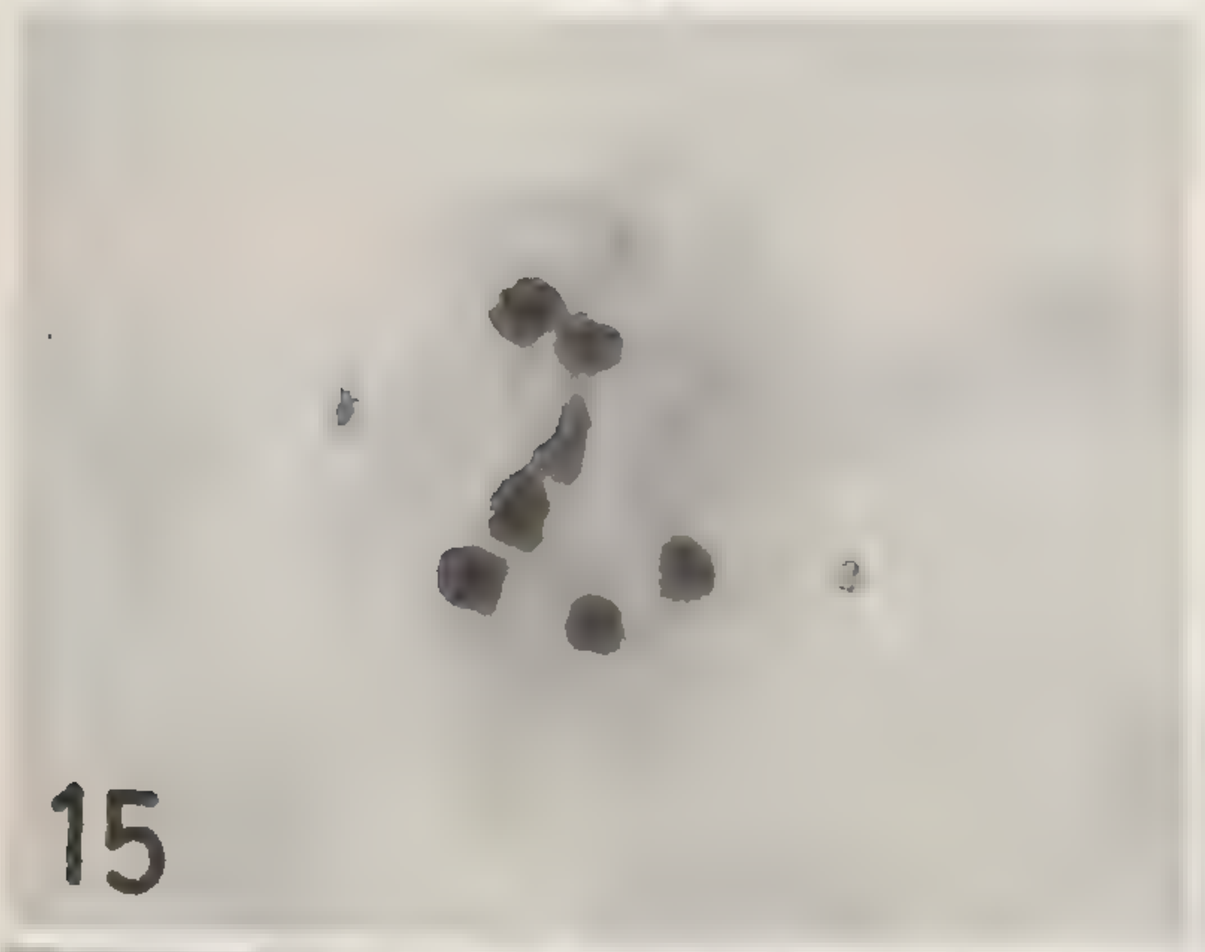
Taxon	Chromosome number n	Basic number x	Voucher
Tribe Triticeae			
**Elymus dahuricus* Turcz. ex Griseb.	21	7	Gilgit: *Omer 2570*
**Elymus semicostatus* (Nees ex Steud.) Melderis (Fig. 17)	14		Chitral: *Ghafoor 2707, 2975*
**Hordeum vulgare* L. (Fig. 18)	$2n = 14$	7	K.U. Campus: *Moin. 31* (seed obtained from NARC, Islamabad)

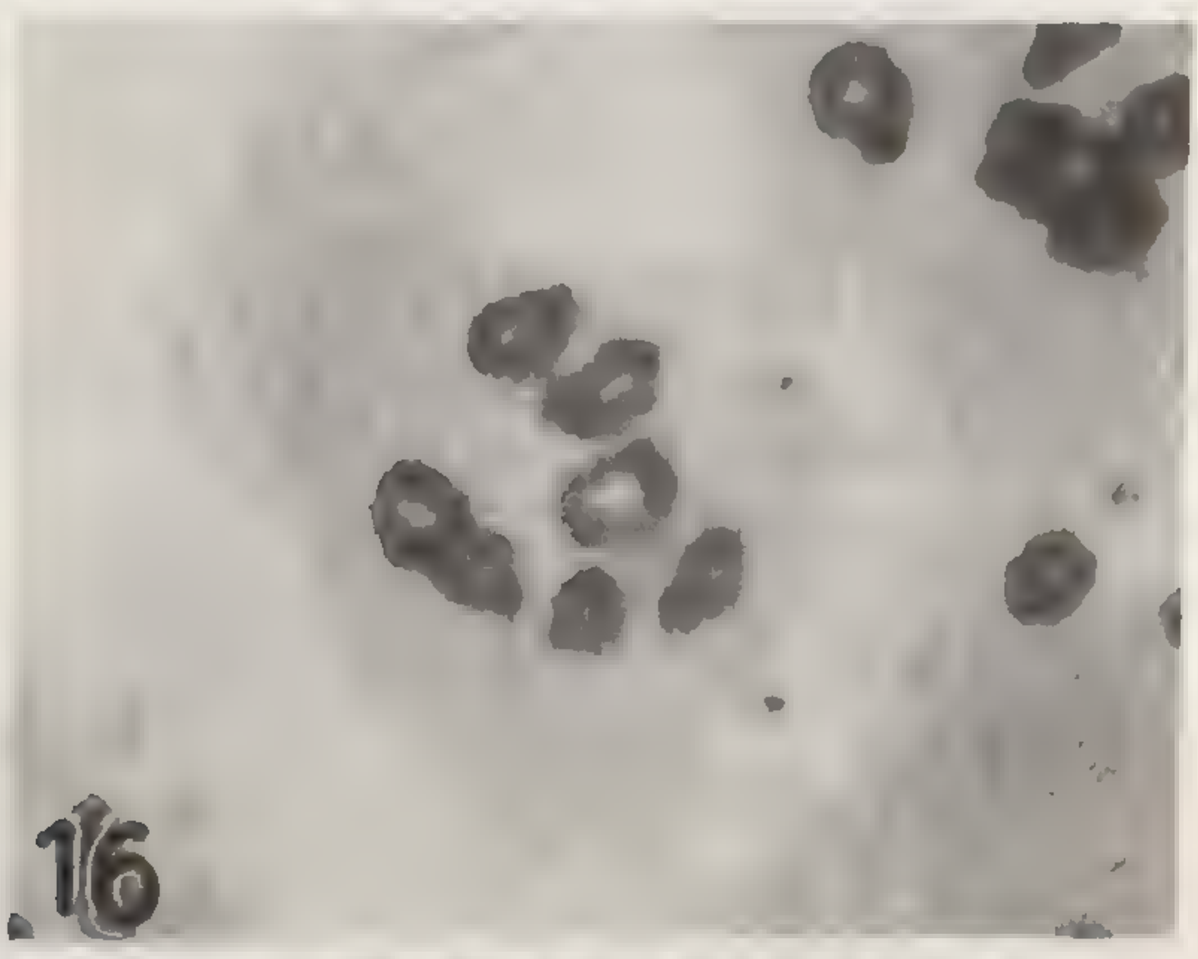
* Count new to flora of Pakistan.
** Count reported for the first time.

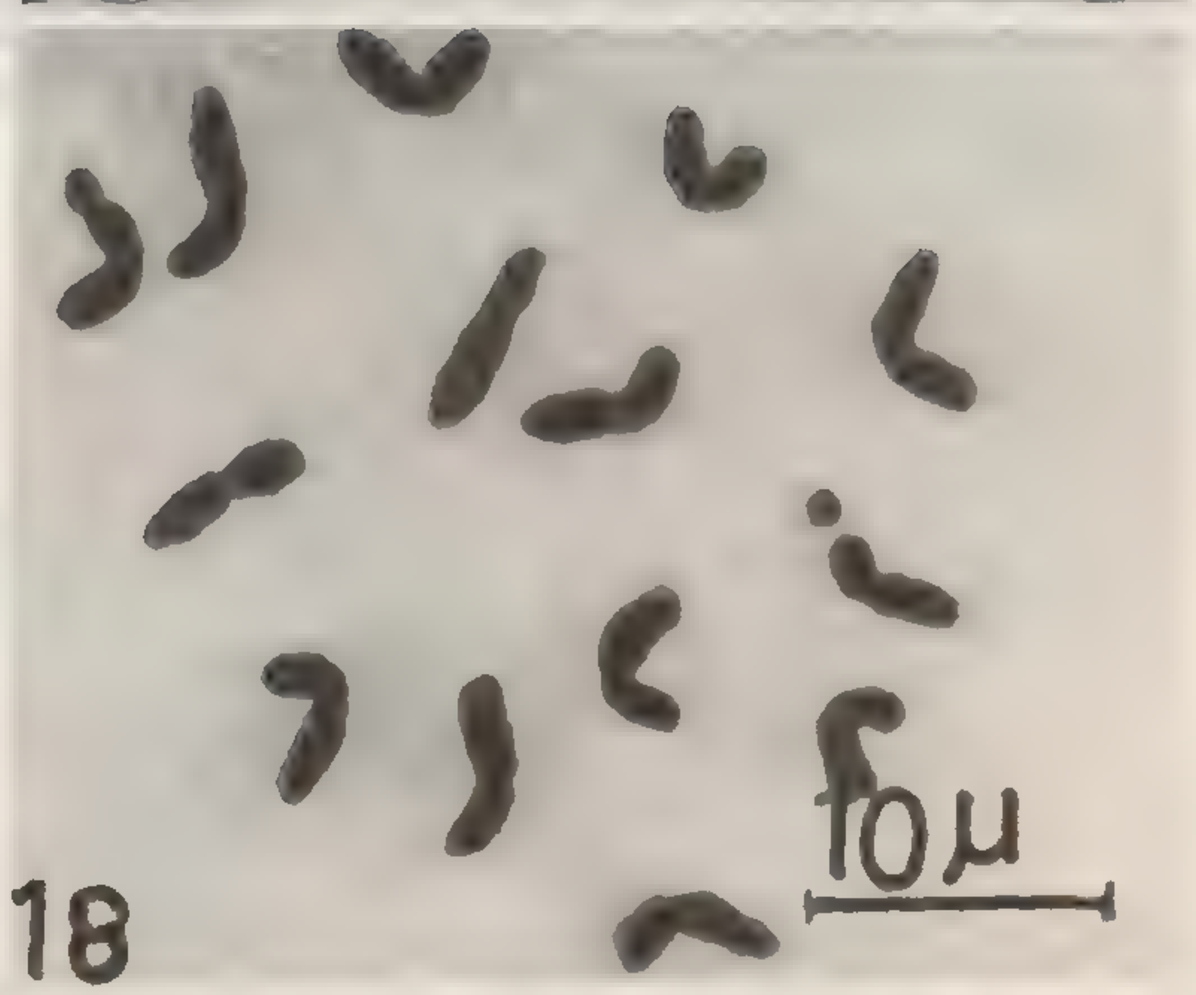












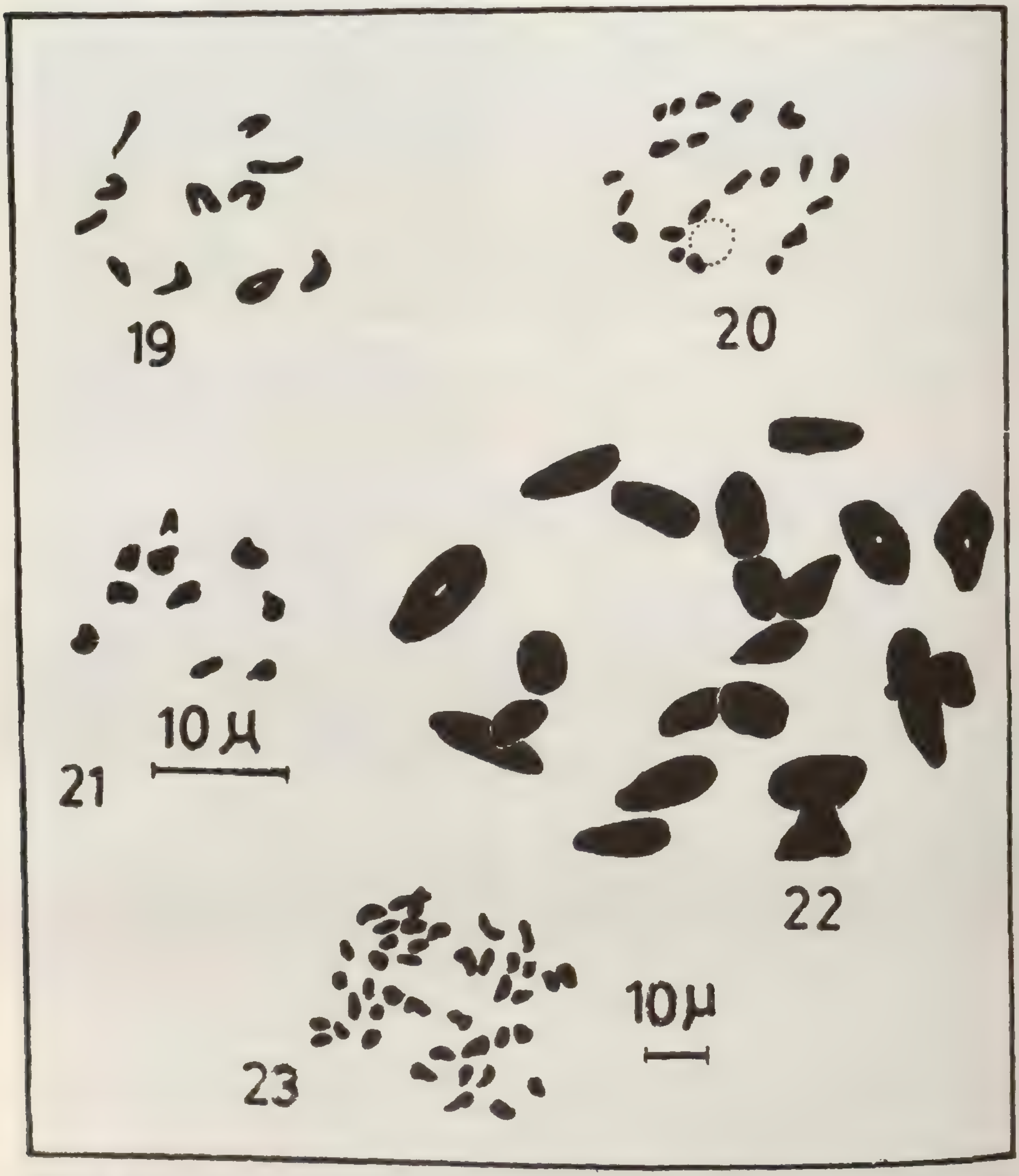
FIGURES 13-18. Chromosomes in members of Poaceae. — 13. *Schismus barbatus* (*Ghafoor 2693*), diakinesis $n = 6$. — 14. *Cynodon dactylon* (*Siddiqui 90*), metaphase-I $n = 9$. — 15. *Bromus danthoniae* (*Ghafoor 2916*), metaphase-I $n = 7$. — 16. *Bromus tectorum* (*Ghafoor 2606*) diakinesis $n = 7$. — 17. *Elymus semicostatus* (*Ghafoor 2707*), diakinesis $n = 14$. 18. *Hordeum vulgare* (*Moin. 31*), mitotic metaphase $2n = 14$.

Diplachne fusca, whereas our material showed $n = 20$ (Fig. 2). This 4*x* cytotype in *D. fusca* is a new report.

In *Ochthochloa compressa* only tetraploids were reported previously (Hiremath & Chennaveeraiah, 1982). One of the present reports of $n = 10$ (diploid) for this species establishes a new ploidy level (Fig. 3).

←

FIGURES 7–12. Pollen mother cell meiosis in members of Poaceae. — 7. *Lolium rigidum* (*Ghafoor 3274*), diakinesis $n = 7$. — 8. *Poa sinaica* (*Omer 2720*), diakinesis $n = 7$. — 9. *Agrostis viridis* (*Ghafoor 2337*), diakinesis. [Arrows indicate B-chromosomes.] $n = 21 + 2B$. — 10. *Phalaris minor* (*Jahan 19*), diakinesis $n = 14$. — 11. *Polypogon monspeliensis* (*Ghafoor 2598*), metaphase-II $n = 14$. — 12. *Piptatherum gracile* (*Ghafoor 3093*), diakinesis $n = 12$.



FIGURES 19–23. Pollen mother cell meiosis in members of Poaceae.—19. *Aristida funiculata* (*Siddiqui 4*), diakinesis $n = 11$.—20. *Aeluropus lagopoides* (*Siddiqui 150*), diakinesis $n = 20$.—21. *Tetrapogon tenellus* (*Moin. 53*), metaphase-I $n = 10$.—22. *Agrostis munroana* (*Omer 2778*), diakinesis $n = 21$.—23. *Avena barbata* (*Omer 2559*), anaphase-I $n = 21$.

In the genus *Tetrapogon*, chromosome numbers in two species were observed. The count for *Tetrapogon tenellus* is contrary to a previous report, $n = 18$ (Singh & Godward, 1960), however our count agrees with basic number ($x = 10$) for the genus (Table 1, Fig. 21).

Chromosome numbers of four species of *Sporobolus* were determined in the tribe Sporoboleae; all of them have $n = 18$. The counts for *Sporobolus arabicus* (Table 1, Fig. 4) and *S. nervosus* (Table 1, Fig. 5) are reported as new to science.

In Zoysieae, chromosome numbers of three species belonging to two genera were determined. The count for *Leptothrium senegalense* (Table 1, Fig. 6) is reported for the first time.

In subfamily Pooideae, chromosome numbers

for 19 species (belonging to 13 genera) in six tribes were determined. The count for *Poa sinaica* (Table 1, Fig. 8) is reported for the first time.

Chromosome numbers for six species belonging to five genera were determined in Aveneae. In *Agrostis viridis*, we observed 21 bivalents and two B-chromosomes (Fig. 9). A hexaploid cytotype of *Avena barbata* ($n = 21$) is reported for the first time (Fig. 23).

In the tribe Stipeae, the count for *Piptatherum gracile* (Table 1, Fig. 12) is reported for the first time.

Literature Cited

Baquar, S. R. & V. Anjum. 1969. Chromosome behaviour in *Cenchrus* complex from southern West Pakistan. Portuguliae Acta Biologica. XI(3–4): 288–296.

——— & M. Saeed. 1969. Chromosome studies and polyploidy analysis in grasses of West Pakistan I. Caryologia 22: 103–111.

Cope, T. A. 1982. Poaceae. *In:* E. Nasir & S. I. Ali (editors), Flora of W. Pakistan 143: 1–678.

Faruqi, S. A., H. B. Quraish & N. Halai. 1979. Chromosome numbers and some morphological characteristics of some Andropogoneae from Pakistan. Cytologia 44: 585–605.

Fedorov, A. A. (editor). 1974. Chromosome Number of Flowering Plants. Otto Koeltz Science Publishers, West Germany (reprinted).

Goldblatt, P. (editor). 1981. Index to Plant Chromosome Numbers 1975–1978. Monogr. Syst. Bot. Missouri Bot. Gard. 5: 1–553.

———. 1984. Index to Plant Chromosome Numbers 1979–1981. Monogr. Syst. Bot. Missouri Bot. Gard. 8: 1–427.

———. 1985. Index to Plant Chromosome Numbers 1982–1983. Monogr. Syst. Bot. Missouri Bot. Gard. 13: 1–224.

———. 1988. Index to Plant Chromosome Numbers 1984–1985. Monogr. Syst. Bot. Missouri Bot. Gard. 23: 1–264.

Hiremath, S. C. & M. S. Chennaveeraiah. 1982. Cytogenetical studies in the wild and cultivated species of *Eleusine* (Gramineae). Caryologia 35: 57–69.

Larsen, K. 1963. Studies in the Flora of Thailand. 14. Cytological studies in vascular plants of Thailand. Dansk Bot. Ark. 20(3): 211–275.

Moore, R. J. (editor). 1973. Index to Plant Chromosome Numbers for 1967–1971. Regnum Vegetabile 90: 1–539.

———. 1974. Index to Plant Chromosome Numbers for 1972. Regnum Vegetabile 91: 1–108.

Sindhe, A. N. R. 1980. Chromosome Number Reports LXVIII. Taxon 29: 545.

Singh, D. N. & M. B. E. Godward. 1960. Cytological studies in the Graminae. Heredity 15(2–3): 193–199.

Willis, J. C. 1973. A Dictionary of the Flowering Plants and Ferns. Cambridge Univ. Press, Cambridge. (8th edition revised by Airy Shaw.)

CHROMOSOME NUMBERS IN SOME TAXA OF FABACEAE MOSTLY NATIVE TO PAKISTAN[1]

Bushreen Jahan,[2] Ahsan A. Vahidy,[3] and S. I. Ali[2]

Abstract

Chromosome numbers are reported for 60 taxa belonging to 35 genera of Fabaceae; 44 of these are native to Pakistan, while the rest are cultivated. Chromosome numbers of seven taxa viz.: *Argyrolobium stenophyllum* (n = 13); *Astragalus bicuspis* (n = 8); *Astragalus ptilocephalus* (n = 8); *Chesneya parviflora* (n = 8); *Indigofera caerulea* var. *caerulea* (n = 8); *Sophora mollis* subsp. *griffithii* Ali (n = 9); and *Taverniera glabra* (n = 8), are reported for the first time. Counts for 35 additional taxa are the first reports for plants native to Pakistan.

In Pakistan, Fabaceae, the third largest family of flowering plants, is represented by 104 genera and 514 species (Ali, 1973a, b, 1977) of which only 35 species (i.e., 6.8%) have been examined chromosomally (Baquar et al., 1965, 1966; Baquar & Husain, 1967; Baquar & Warsi, 1968; Baquar & Askari, 1970; Quraish & Faruqi, 1970; Faruqi, 1977; Khatoon & Ali, 1982, 1991). The chromosome numbers for 60 taxa belonging to 35 genera of Fabaceae from Pakistan are reported. Counts for seven taxa are reported for the first time and counts for 35 species are new records from this country.

Materials and Methods

The meiotic and mitotic materials (i.e., the floral buds and seeds respectively) of wild species were collected from various regions of Pakistan. A number of cultivated species were also included in our study (Table 1).

For meiotic chromosome counts, floral buds were fixed in Carnoy's solution (3 parts of absolute ethanol: 1 part of glacial acetic acid) for 24 hr. and then stored in a refrigerator. Slides were prepared by routine squash technique using 1% acetocarmine or 1.8% aceto-orcein.

For mitosis, root tips from germinating seeds were pretreated with 0.002 M 8-OH quinoline (for 4–6 hr.), fixed in Carnoy's solution for 1 hr., hydrolysed in 1 N HCl for 6–12 min. and squashed in 1.8% aceto-orcein.

Most photomicrographs were taken from temporary mounts. Preparations were made permanent by mounting in euparal. Voucher specimens, identified with the help of the Flora of Karachi (Jafri, 1966) and the Flora of Pakistan (Ali, 1973a, b, 1977), are deposited in Karachi University Herbarium (KUH).

Observations and Results

Chromosome counts for 60 taxa in 17 tribes of Fabaceae are presented in Table 1. Counts new to science and new to the flora of Pakistan are specified on the basis of a survey of IPCN (Moore, 1973; Fedorov, 1974; Goldblatt, 1981b, 1984, 1985, 1988). The tribes are arranged according to Goldblatt (1981a).

Discussion

In the present study most of the chromosome counts that are in conformity with earlier reports have not been commented upon.

In Sophoreae, *Sophora mollis* subsp. *griffithii* has n = 9 (Fig. 1), reported here for the first time. This accords with the most frequent number in the genus in which n = 14, 11, 9, and possibly 8 have also been found (Goldblatt, 1981a).

In Tephrosieae, *Milletia peguensis* has n = 11, corresponding with the basic number x = 11 suggested by Goldblatt (1981a) for the tribe. *Tephro-*

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TABLE 1. Chromosome numbers in Fabaceae. K.U. = Karachi University. D. G. Khan = town of Dera Ghazi Khan.

Taxon	Chromosome number n	Basic number x	Voucher
Subfamily Caesalpinioideae			
Tribe Caesalpinieae			
Parkinsonia aculeata L. (cultivated)	14	14	K.U. Campus: *Siddiqui 36*
Tribe Cassieae			
Cassia holosericea Fresen	14	14	K.U. Campus: *Siddiqui 1*
**Cassia occidentalis* L. (cultivated)	14		K.U. Campus: *Jahan 13*; Hasanabdal: *Ghafoor 3889*
Subfamily Mimosoideae			
Tribe Ingeae			
**Pithecellobium dulce* (Roxb.) Benth. (cultivated)	13	13	K.U. Campus: *Siddiqui 17*
Subfamily Papilionoideae			
Tribe Sophoreae			
***Sophora mollis* (Royle) Baker subsp. *griffithii* (Stocks) Ali (Fig. 1)	9	9	Panjgur: *Omer 2057*
Tribe Tephrosieae			
**Millettia peguensis* Ali (cultivated)	11	11	K.U. Campus: *Siddiqui 35*
**Tephrosia apollinea* (Delile) Link (Fig. 2)	22	11	Khushab: *Ghafoor 3762*
**Tephrosia purpurea* (L.) Pers.	11	11	Kashmir: *T. Ali 15*; Layyah: *Ghafoor 3735*
Tephrosia purpurea	22		Makran: *Omer 2106*
Tephrosia strigosa (Dalzell) Sant. & Maheshw.	11	11	K.U. Campus: *Jahan 32*
Tephrosia subtriflora Baker	11		K.U. Campus: *Siddiqui 10, 54, Jahan 56, 47*; Safari Park, Karachi: *Siddiqui 68, Jahan 24*
Tribe Robinieae			
**Gliricidia sepium* (Jacq.) Steud. (cultivated)	11	11	K.U. Campus: *Siddiqui 23*
**Sesbania bispinosa* (Jacq.) W. Wight	6	6	Kathore: *Jahan 71*
**Sesbania sesban* (L.) Merrill (cultivated)	6, $2n = 12$		Darsanochano: *Siddiqui 93*; Safari Park, Karachi: *Siddiqui 59*; Sajawal: *Ahsan 22*
Tribe Indigofereae			
Cyamopsis tetragonoloba (L.) Taubert (cultivated) (Figs. 3 & 4)	7	7	Bhawalpur: *Ghafoor 3577*; Muzaffargarh: *Ghafoor 3606*; K.U. Campus: *Moin. 61*
***Indigofera caerulea* Roxb. var. *caerulea* (Fig. 5)	8	8	K.U. Campus: *Siddiqui 37*
**Indigofera cordifolia* Heyne ex Roth	8		K.U. Campus: *Ahsan 4*; D. G. Khan: *Ghafoor 3730*
Indigofera hochstetteri Baker (Fig. 6)	8		Bawana: *Ghafoor 3689*; Darsanochano: *Jahan 31*; Kathore: *Jahan 70*; K.U. Campus: *Razaq 140*

TABLE 1. Continued.

Taxon	Chromosome number n	Basic number x	Voucher
Indigofera oblongifolia Forssk.	8		K.U. Campus: *Siddiqui 16, 52*; Safari Park, Karachi: *Siddiqui 66*; Darsanochano: *Siddiqui 77*; Thatta: *Siddiqui 107*
Tribe Desmodieae			
Alysicarpus heterophyllus (Baker) Jafri & Ali (Fig. 7)	8	8	K.U. Campus: *Moin. 45*
Alysicarpus monilifer (L.) DC.	8		K.U. Campus: *Siddiqui 27, Ahsan 2*
**Alysicarpus ovalifolius* (Schumach.) J. Léonard	8		K.U. Campus: *Moin. 60*
**Alysicarpus rugosus* (Willd.) DC.	8		Ghotki: *Ghofoor 3515*
**Desmodium elegans* DC.	11	11	Kashmir: *T. Ali 236*
**Desmodium gangeticum* (L.) DC.	11		Kashmir: *T. Ali 130*
**Lespedeza juncea* (L.f.) Pers. var. *sericea* (Thunb.) Lace & Hemsl.	10	10	Kashmir: *T. Ali 471*
Tribe Phaseoleae			
**Cajanus cajan* (L.) Millsp. (cultivated)	11	11	K.U. Campus: *Moin. 11*
**Clitoria ternatea* L.	8	8	Malir, Karachi: *Moin. 19*
**Flemingia fruticulosa* Wall. ex Benth.	11	11	Murree: *Ghafoor 4135*
**Glycine max* (L.) Merrill (cultivated)	20	20	K.U. Campus: *Razaq 137*
**Phaseolus vulgaris* L. (cultivated)	11	11	D. G. Khan: *Ghafoor 3690*
**Rhynchosia capitata* (Heyne ex Roth) DC.	11	11	K.U. Campus: *Razaq 131*
Rhynchosia minima (L.) DC.	11		K.U. Campus: *Siddiqui 18*
Rhynchosia pulverulenta Stocks	11		K.U. Campus: *Siddiqui 38*
**Vigna mungo* (L.) Hepper (cultivated)	$2n = 22$	11	K.U. Campus: *Moin. 29*
**Vigna trilobata* (L.) Verdc.	11		K.U. Campus: *Razaq, 129*; Manghopir: *Razaq 155*
**Vigna unguiculata* (L.) Walp. subsp. *unguiculata* (cultivated)	11		K.U. Campus: *Razaq 136*
Tribe Aeschynomeneae			
**Arachis hypogaea* L. (cultivated)	20	10	K.U. Campus: *Razaq 130*
Tribe Galegeae			
Alhagi maurorum Medikus	8	8	K.U. Campus: *Moin. 14*; Sajawal: *Ahsan 25*; Thatta: *Siddiqui 96, 128, 147*
***Astragalus bicuspis* Fisch. (Figs. 8a & b)	8	8	Gilgit: *Omer 2470*
**Astragalus leucocephalus* Graham ex Benth.	8		Shangla, N.W.F.P.; *Ghafoor 4008*
***Astragalus ptilocephalus* Baker	8		Chitral: *Ghafoor 2567*

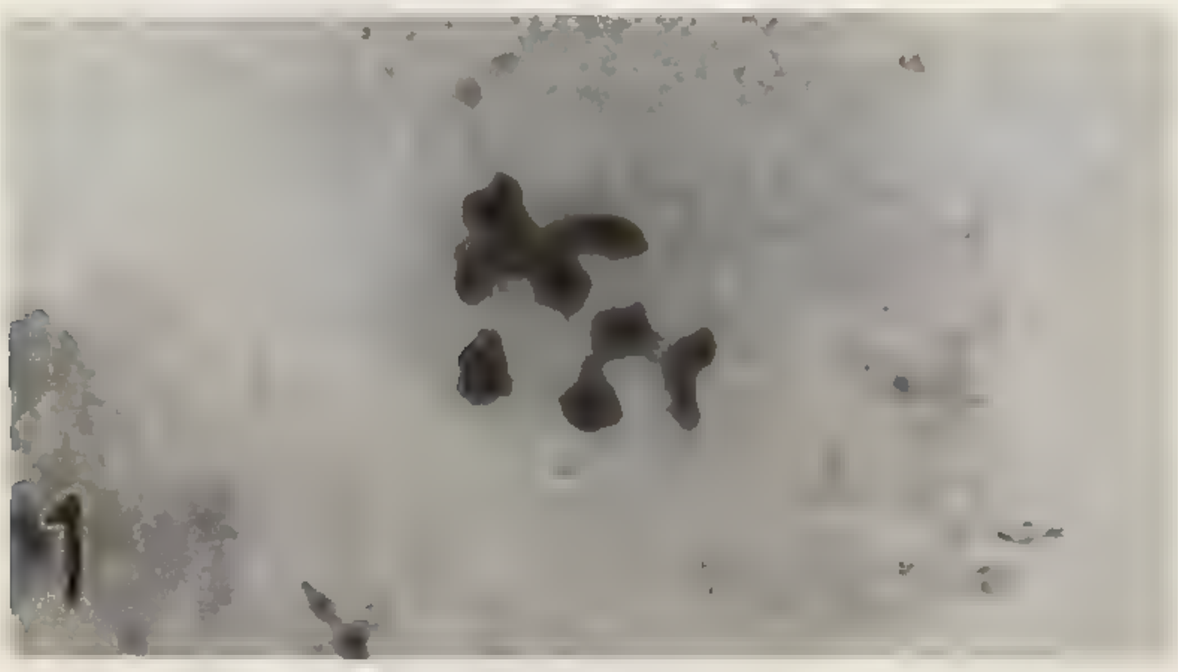
TABLE 1. Continued.

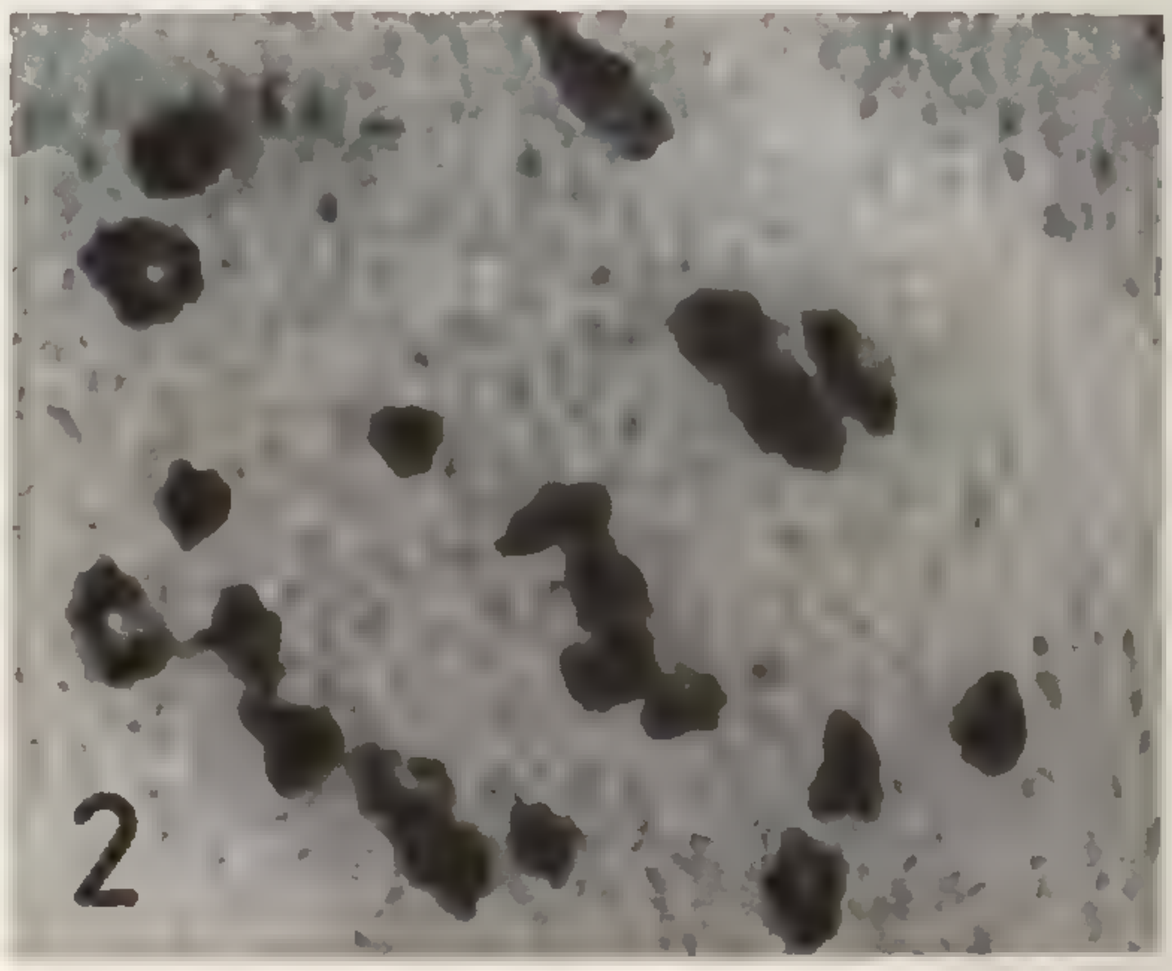
Taxon	Chromosome number n	Basic number x	Voucher
****Chesneya parviflora** Jaub. & Spach (Fig. 9)	8	8	Panjgur: *Omer 2076*
***Oxytropis lapponica** (Wahl) Gay	8	8	Chitral: *Ghafoor 3154*
Tribe Hedysareae			
Taverniera cuneifolia (Roth) Arn. (Fig. 10)	8	8	K.U. Campus: *Ahsan 54*
****Taverniera glabra** Boiss. (Fig. 11)	8	8	Panjgur: *Omer 2073*
Tribe Vicieae			
***Lathyrus aphaca** L. (Fig. 12)	7	7	K.U. Campus: *Razaq 149*
***Vicia faba** L. (cultivated)	6	6	Chitral: *Ghafoor 3200*
Tribe Cicereae			
***Cicer arietinum** L. (cultivated)	8	8	K.U. Campus: *Moin. 28*
Tribe Trifolieae			
***Medicago falcata** L.	16	8	Astor: *Omer 2311*
***Medicago lupulina** L.	8		K.U. Campus: *Siddiqui 30*; Dir: *Ghafoor 2426*; Swat: *Ghafoor 4007*
Medicago sativa L.	8		Thatta: *Siddiqui 104*
Medicago sativa	16		Chitral: *Ghafoor 2848, 3108*; K.U. Campus: *Jahan 16*; Mustuj: *Ghafoor 3003*; Arkari: *Ghafoor 2799*
Melilotus alba Desr.	8	8	K.U. Campus: *Siddiqui 28*; Thatta: *Siddiqui 127, 113*
Melilotus indica (L.) All.	8		K.U. Campus: *Siddiqui 6*; Thatta: *Siddiqui 125*; Darsanochano: *Siddiqui 92*
Melilotus officinalis (L.) Pall.	8		Astor: *Omer 2428*; Naltar: *Omer 2582*; Avarik: *Ghafoor 2735*
***Trifolium resupinatum** L. (Fig. 13)	8	8	Malakand: *Ghafoor 3914*; Thatta: *Siddiqui 140*
***Trigonella foenum-graecum** L. (cultivated) (Fig. 14)	$2n = 16$	8	K.U. Campus: *Moin. 24*
Tribe Crotalarieae			
Crotalaria burhia Buch.-Ham. ex Benth.	8	8	K.U. Campus: *Siddiqui 47, 51*; Cholistan: *Ghafoor 3543*; Darsanochano: *Siddiqui 75*
***Crotalaria juncea** L. (Fig. 15)	8		Khushab: *Ghafoor 3813*
***Crotalaria medicaginea** Lam. var. *medicaginea* (Fig. 16)	16		Kashmir: *T. Ali 390*
Tribe Genisteae			
****Argyrolobium stenophyllum** Boiss. (Fig. 17)	13	13	Khushab: *Ghafoor 3829*

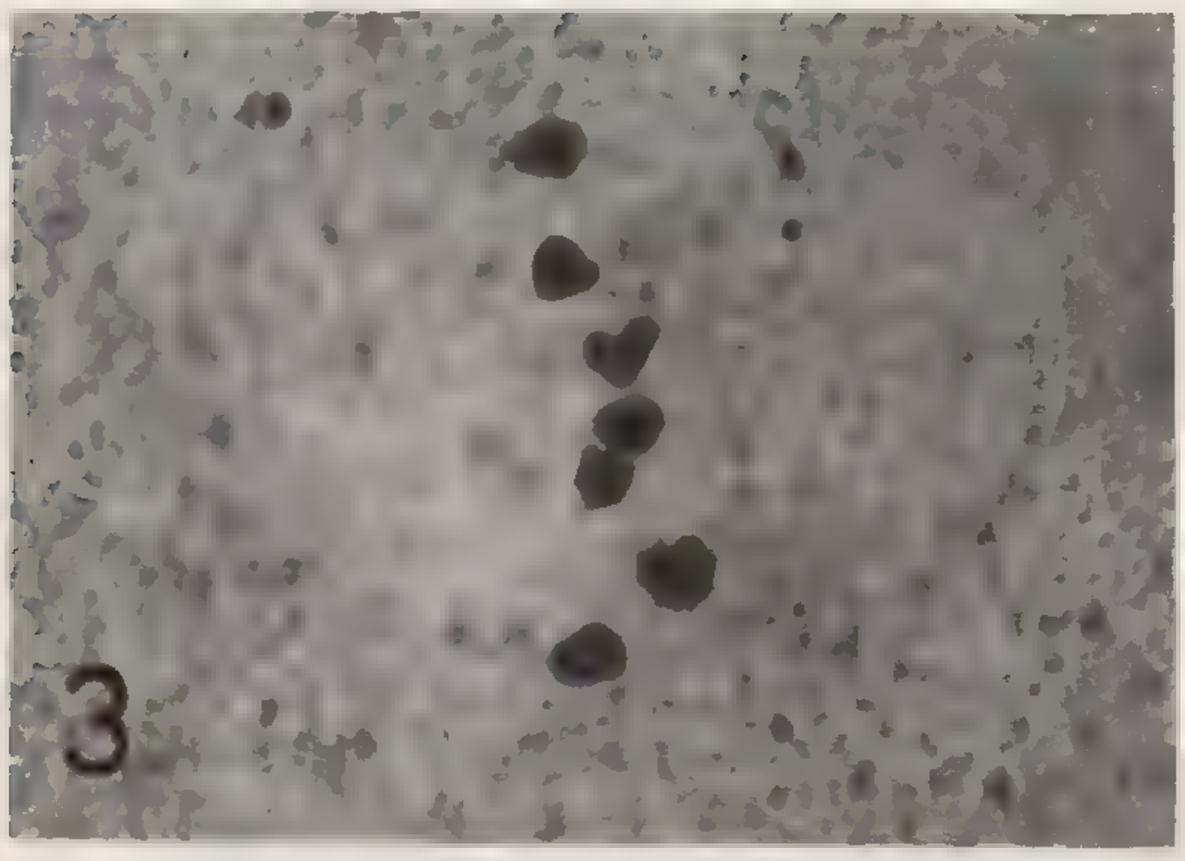
* Count new to flora of Pakistan.
** Count being reported for the first time.

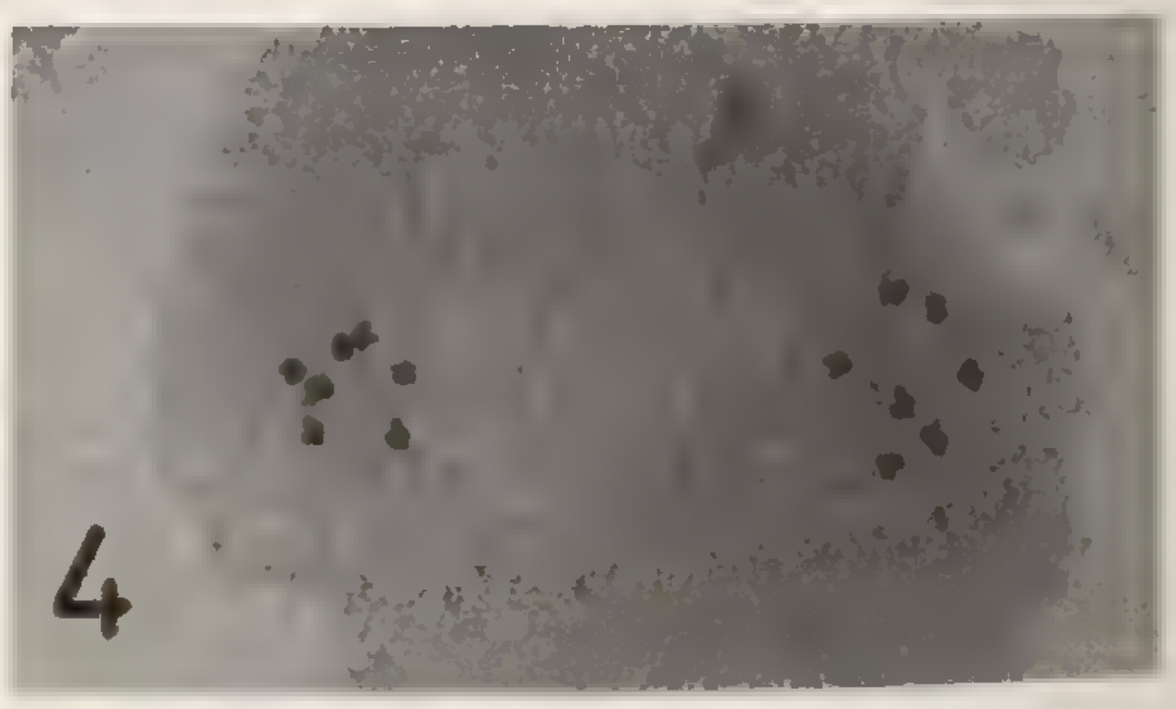
sia subtriflora and *T. strigosa* also have $n = 11$, while *T. purpurea* has both $n = 11$ and $n = 22$, confirming the observations of Srivastav & Raina (1986). In *T. apollinea* we find $n = 22$ (Fig. 2), previously reported as $n = 11$ (Srivastav & Raina, 1986); therefore the present report is the first of a tetraploid cytotype in this species.

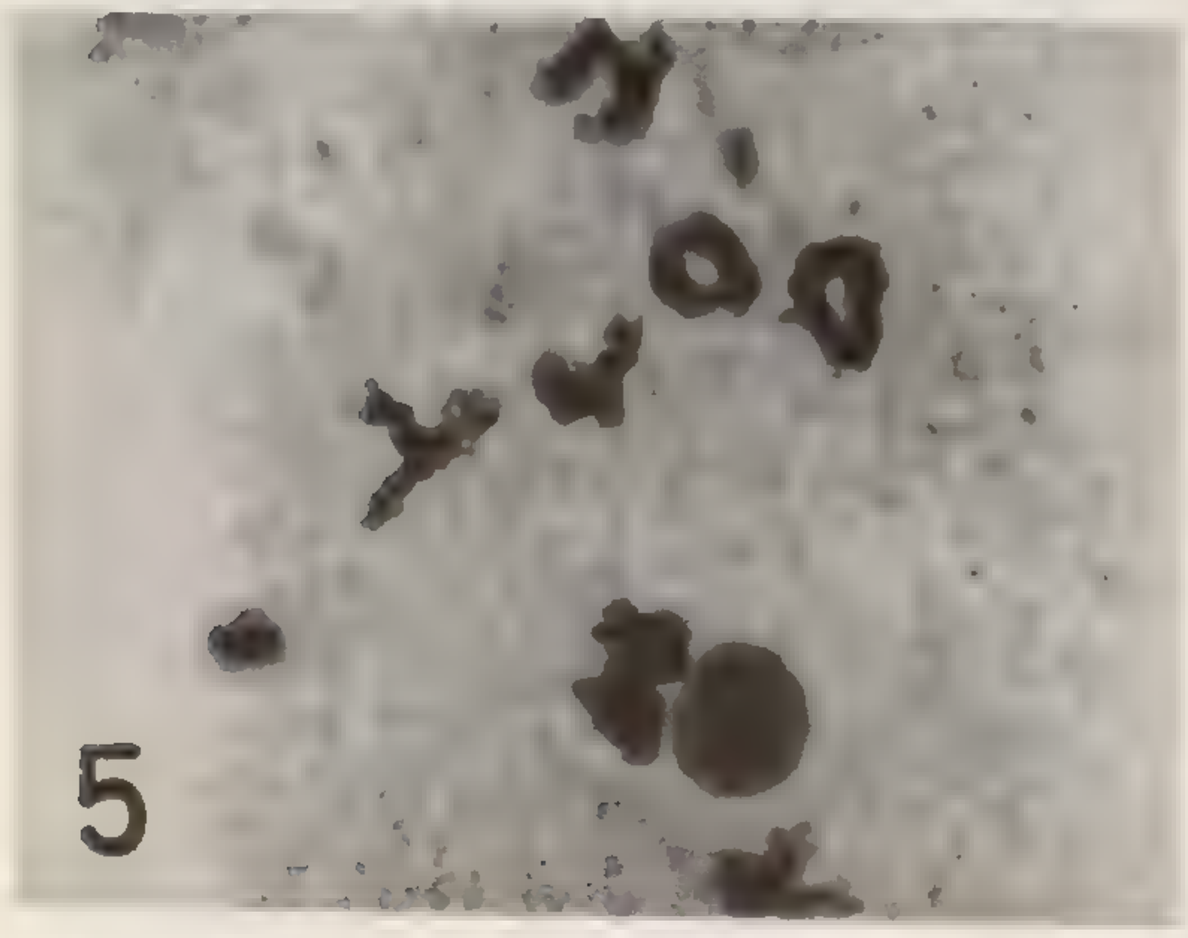
In Robineae, *Gliricidia sepium* has $n = 11$.

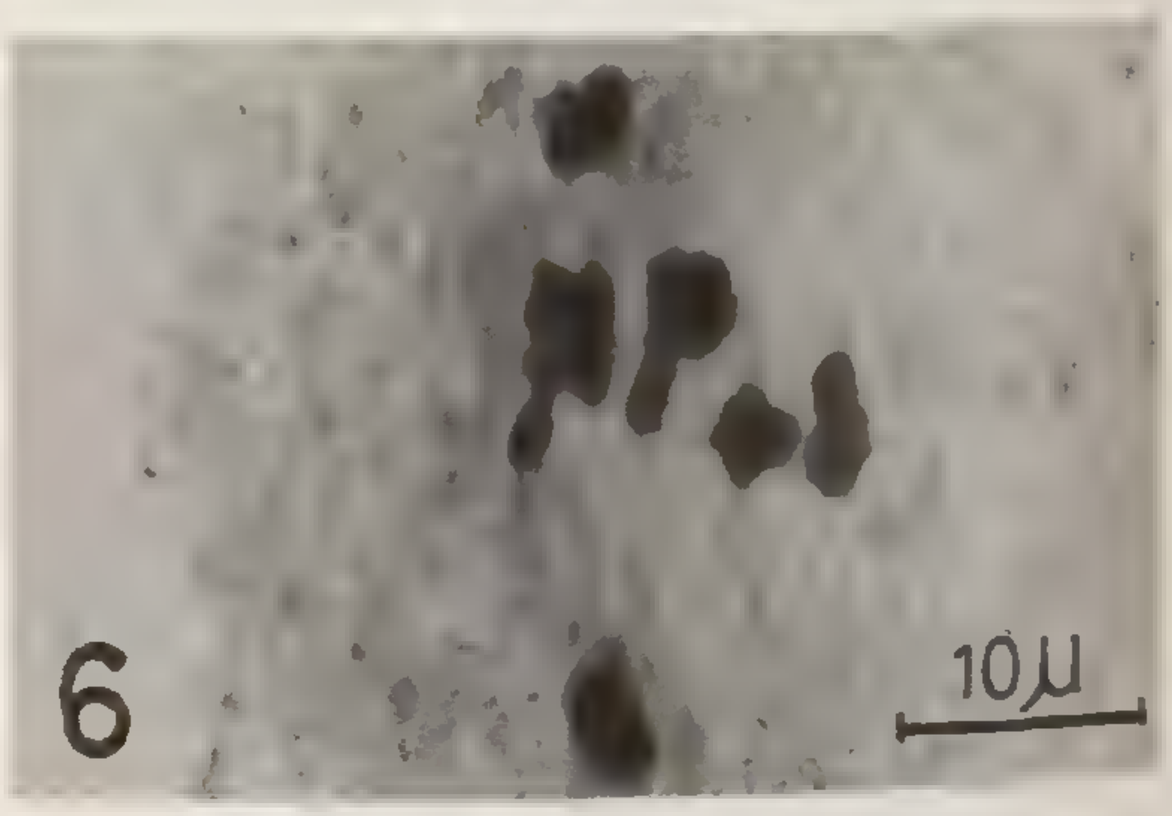












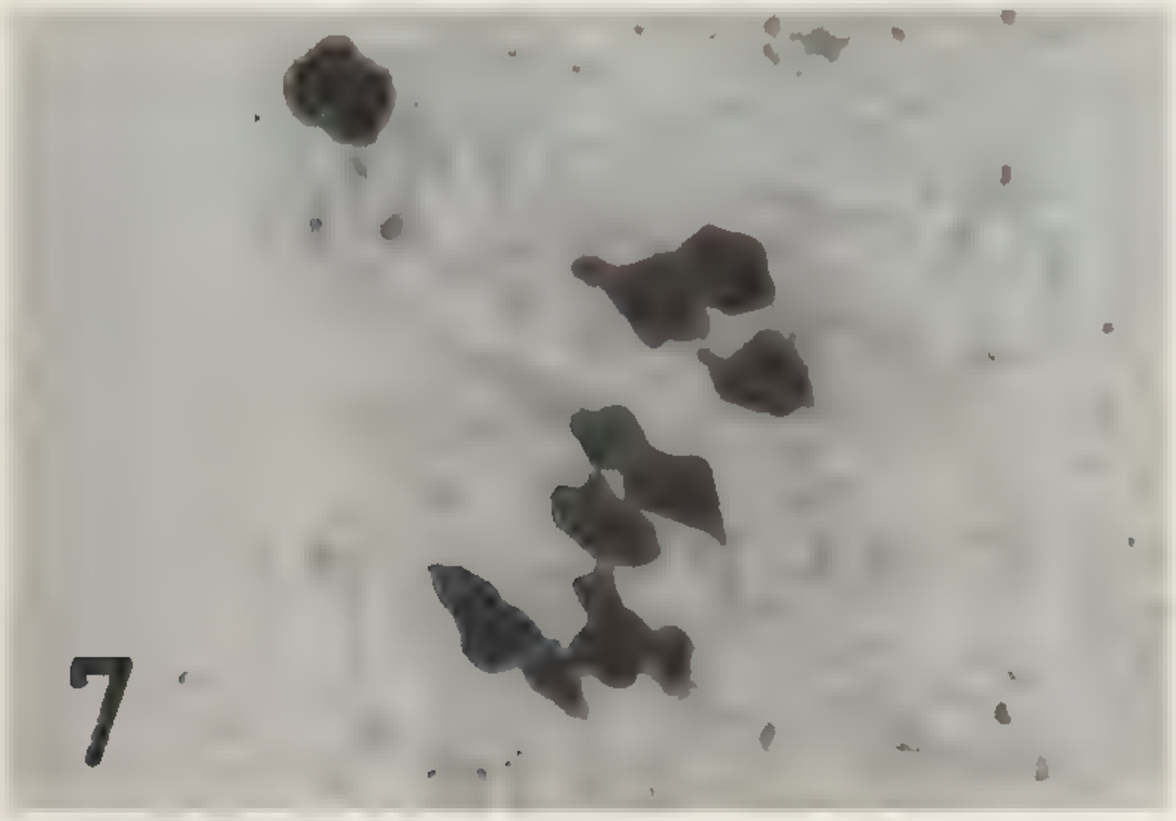
FIGURES 1–6. Pollen mother cell meiosis in members of Fabaceae.—1. *Sophora mollis* subsp. *griffithii* (*Omer 2057*), metaphase I, $n = 9$.—2. *Tephrosia apollinea* (*Ghafoor 3762*), diakinesis, $n = 22$.—3. *Cyamopsis tetragonoloba* (*Ghafoor 3577*), metaphase I, $n = 7$.—4. *Cyamopsis tetragonoloba* (*Ghafoor 3606*), metaphase II, $n = 7$.—5. *Indigofera caerulea* var. *caerulea* (*Siddiqui 37*), diakinesis, $n = 8$.—6. *Indigofera hochstetteri* (*Ghafoor 3689*), metaphase I, $n = 8$.

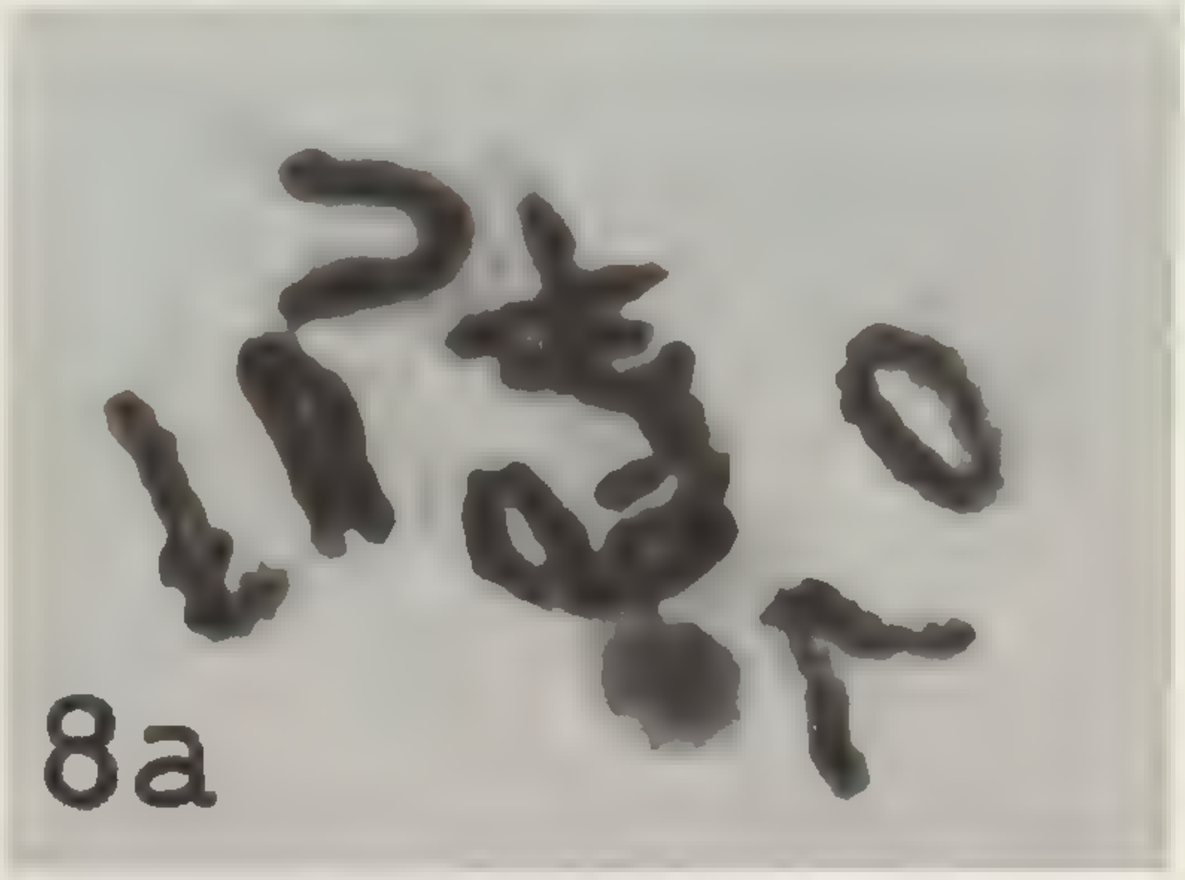
Both $n = 11$ and 10 have been reported for many cultivated species (Goldblatt, 1981a).

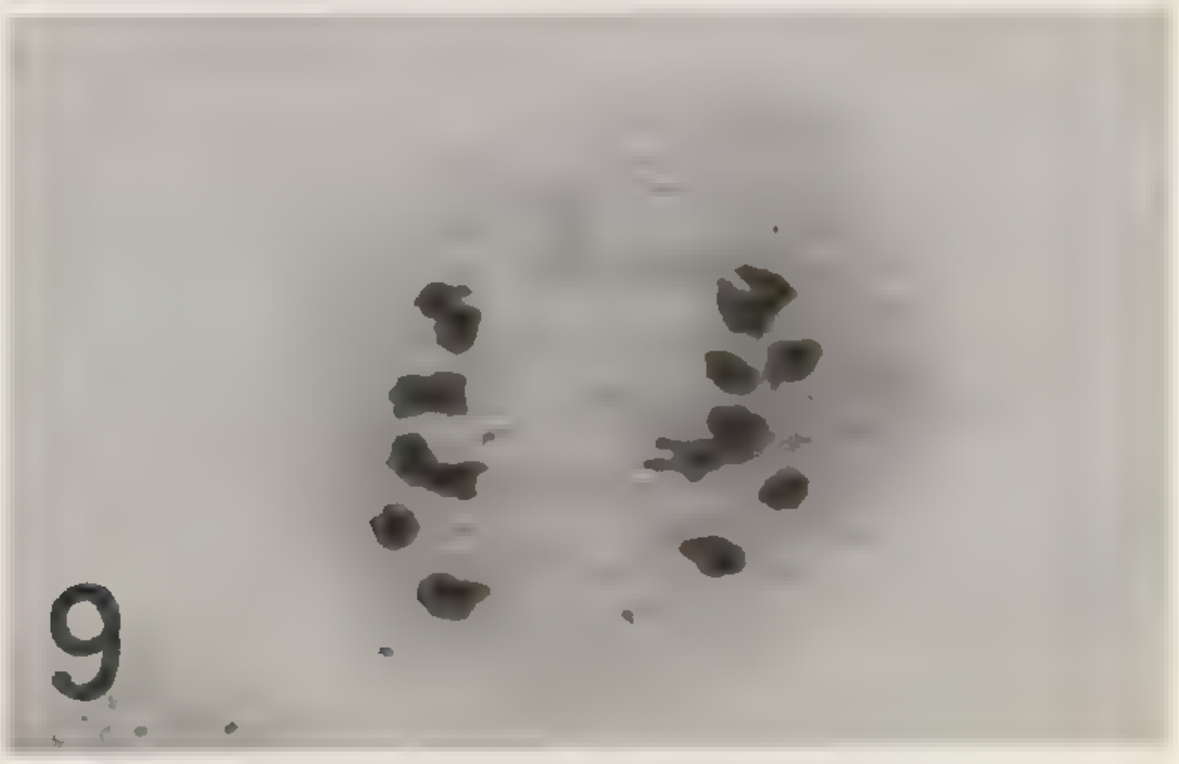
In Indigofereae, four species of *Indigofera* examined have $n = 8$ (Table 1), corresponding to the base number for the genus (Goldblatt, 1981a). The count for *Indigofera caerulea* var. *caerulea* ($n = 8$; Fig. 5) is the first report for this species.

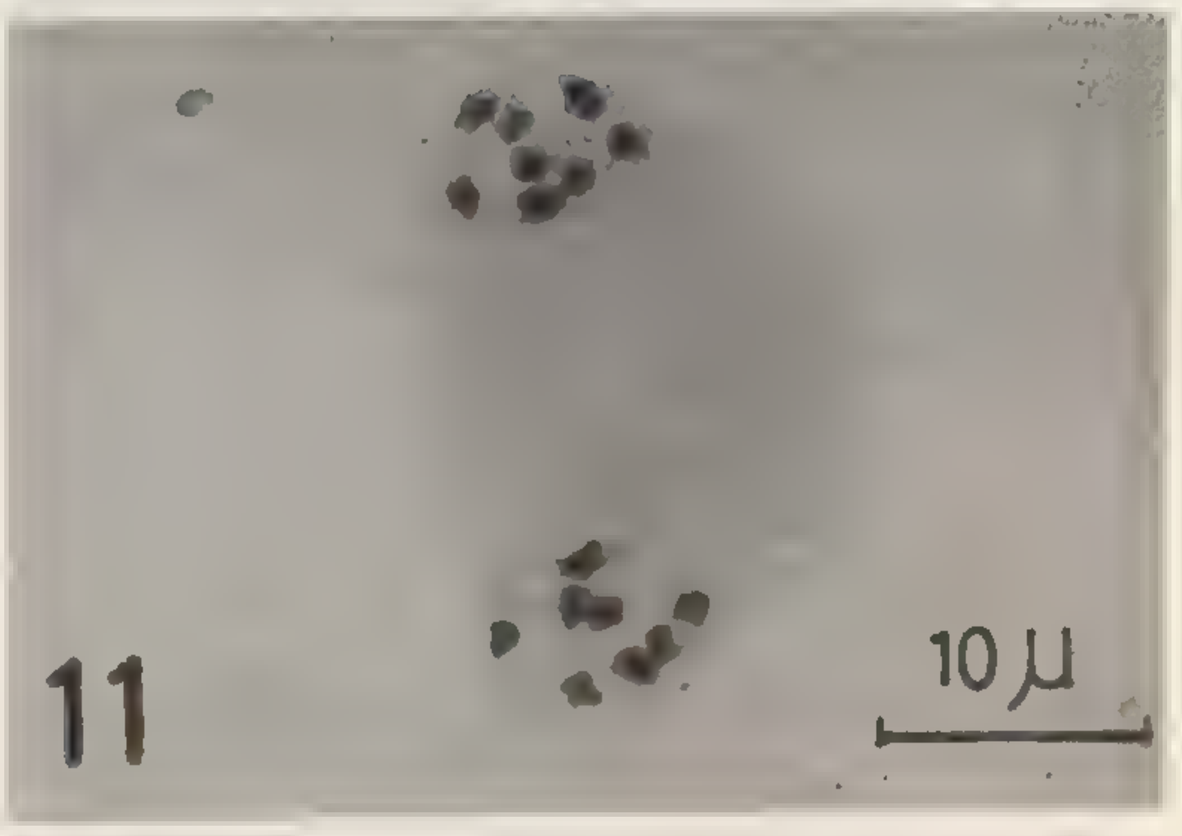
Most genera studied by us in Phaseoleae have $n = 11$, except *Glycine max* with $n = 20$ and *Clitoria ternatea* with $n = 8$ (Table 1). Counts of $x = 11$ are the most common base number reported in the literature for this tribe (Goldblatt, 1981a) in which $x = 11$ is almost certainly basic.

In Galegeae, all of our accessions of *Alhagi maurorum* have $n = 8$, which accords with earlier records (Amin, 1979; Khatoon & Ali, 1990). Our observations of $n = 8$ in *Astragalus bicuspis* (Fig. 8a & b) and $n = 8$ in *Chesneya parviflora* (Fig. 9) are first chromosome number determinations for these species.









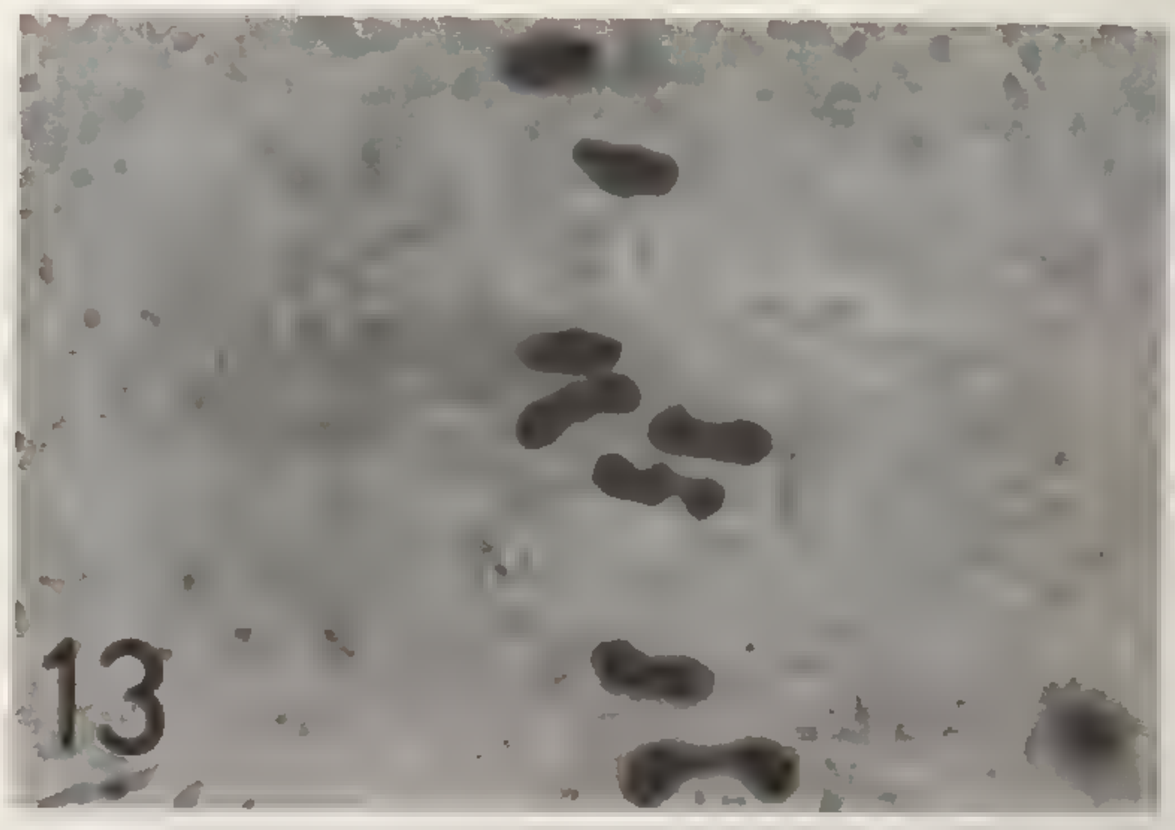
FIGURES 7–11. Pollen mother cell meiosis in members of Fabaceae.—7. *Alysicarpus heterophyllus* (*Moin. 45*), metaphase I, $n = 8$.—8a. *Astragalus bicuspis* (*Omer 2470*), diakinesis, $n = 8$.—8b. *Astragalus bicuspis* (*Omer 2470*), metaphase I, $n = 8$.—9. *Chesneya parviflora* (*Omer 2076*), early anaphase I, $n = 8$.—10. *Taverniera cuneifolia* (*Ahsan 54*), late anaphase I, $n = 8$.—11. *Taverniera glabra* (*Omer 2073*), late anaphase I, $n = 8$.

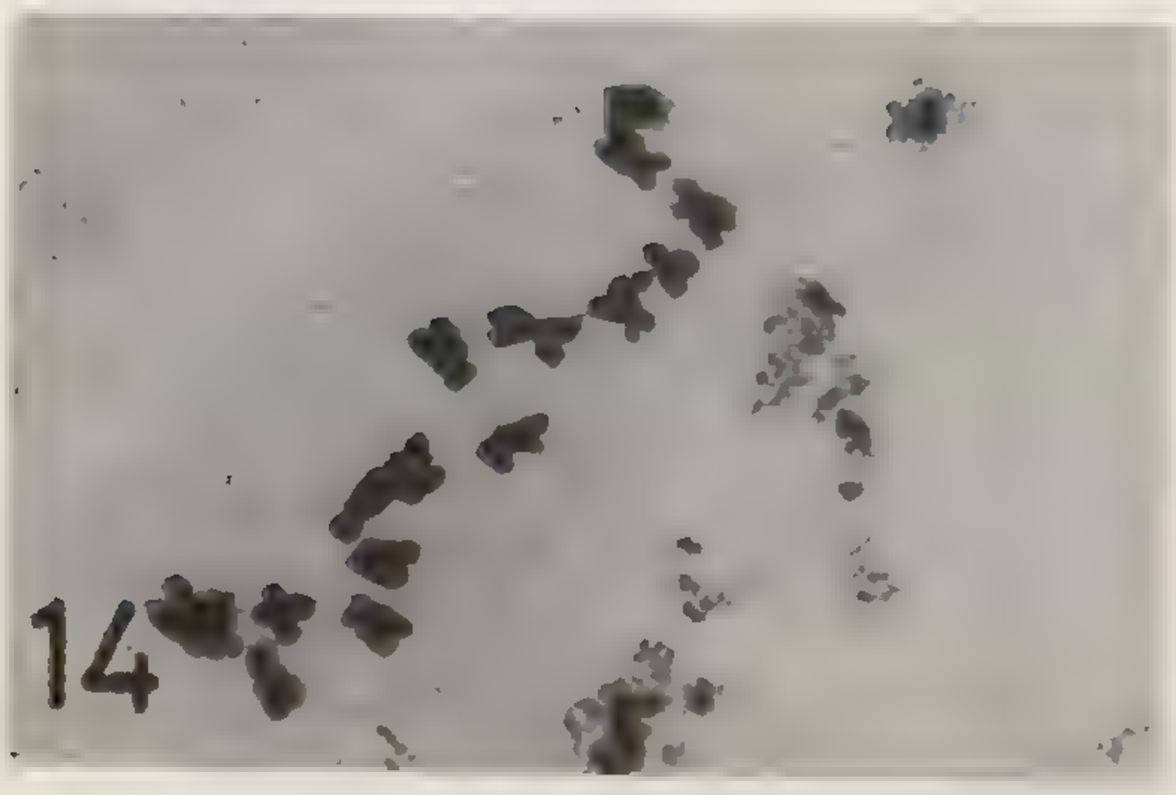
Chromosome numbers of two species of *Taverniera* (Hedysareae) have $n = 8$, consistent with the basic number for the tribe (Goldblatt, 1981a). The present count for *T. glabra* ($n = 8$; Fig. 11) is new to science.

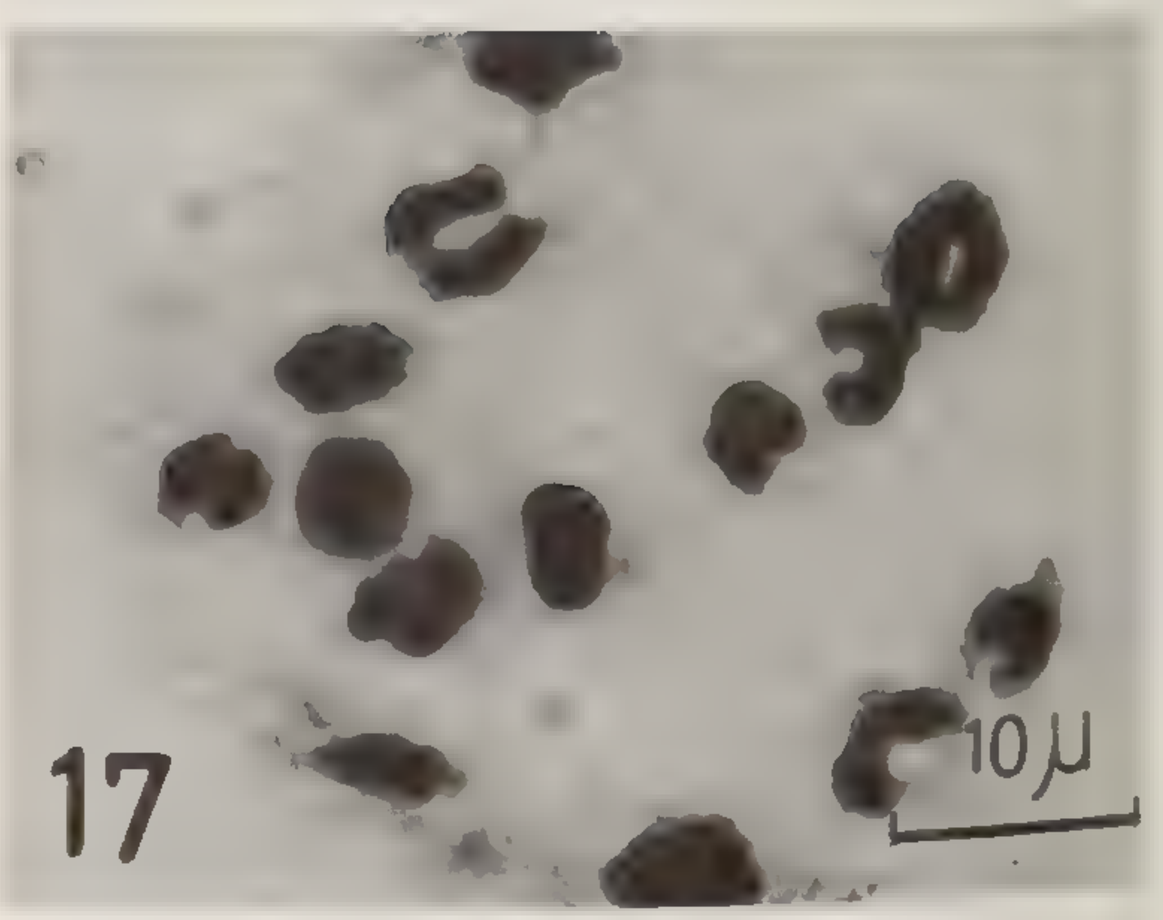
In the monogeneric Cicereae our count of $n = 8$ for *Cicer arietinum* confirms the basic number ($x = 8$) for the species and tribe (Goldblatt, 1981a).

Trifolieae are important in agriculture and already well studied cytologically. *Medicago falcata* and *M. sativa* have polyploid races. *Medicago falcata* has diploid and tetraploid cytotypes, but the material studied by us is at tetraploid level only. *Medicago sativa* has been extensively studied by various workers, and cytotypes from $2x$ to $8x$ have been reported in the literature. We found two cytotypes, i.e., $2x$ and $4x$, in our accessions. We did not find any polyploid in the rest of the genera of this tribe.

In Crotalarieae our counts for three species of







FIGURES 12–17. Pollen mother cell meiotic and root tip mitotic chromosomes in members of Fabaceae.—12. *Lathyrus aphaca* (*Razaq 149*), metaphase I, $n = 7$.—13. *Trifolium resupinatum* (*Ghafoor 3914*), metaphase I, $n = 8$.—14. *Trigonella foenum-graecum* (*Moin. 24*), mitotic metaphase, $2n = 16$.—15. *Crotalaria juncea* (*Ghafoor 3813*), metaphase II, $n = 8$.—16. *Crotalaria medicaginea* var. *medicaginea* (*T. Ali 390*) prophase II, $n = 16$.—17. *Argyrolobium stenophyllum* (*Ghafoor 3829*), diakinesis, $n = 13$.

Crotalaria (Table 1) confirm the earlier reports for the species (Bir & Kumari, 1978; Khatoon & Ali, 1991). In *C. medicaginea* (Fig. 16) both diploids and tetraploids are recorded (Bir & Sidhu, 1975; Bir & Kumari, 1978).

In Genisteae the count for *Argyrolobium stenophyllum*, $n = 13$ (Fig. 17), is the first for the species. Goldblatt (1981a) suggested $x = 8$ as the base number for this genus and regards the gametic numbers 15 and 13 as hypotetraploid.

LITERATURE CITED

ALI, S. I. 1973a. Mimosaceae. *In:* E. Nasir & S. I. Ali (editors), Flora of Pakistan 36: 1–40.

———. 1973b. Caesalpiniaceae. *In:* E. Nasir & S. I. Ali (editors), Flora of Pakistan 54: 1–47.

———. 1977. Papilionaceae. *In:* E. Nasir & S. I. Ali (editors), Flora of Pakistan 100: 1–389.

AMIN, A. 1979. Chromosome numbers of ten flowering plants of Egypt. U.A.R. J. Bot. 22: 73–75.

BAQUAR, S. R. & S. H. A. ASKARI. 1970. Chromosome studies in some flowering plants of West Pakistan. II. Genét. Ibér. 22: 41–51.

——— & A. Husain. 1967. Chromosome studies in some flowering plants of West Pakistan. I. Phyton (Buenos Aires) 24: 49–55.

——— & B. A. Warsi. 1968. Chromosome Number Reports XV. Taxon 17: 91–104.

———, S. Akhtar & A. Husain. 1965. Meiotic chromosome numbers in some vascular plants of the Indus delta. I. Bot. Not. 118: 289–298.

———, A. Husain & S. Akhtar. 1966. Meiotic chromosome numbers in some vascular plants of the Indus delta. II. Bot. Not. 119: 24–32.

Bir, S. S. & S. Kumari. 1978. Chromosome Number Reports LIX. Taxon 27: 53–61.

——— & M. Sidhu. 1975. Weed flora of cultivable lands in Punjab maize fields in Patiala district. Acta Bot. Indica 3: 136–141.

Faruqi, S. A.. 1977. Chromosome numbers of some plants from Pakistan. Libyan J. Sci. 7A: 71–72

Fedorov, A. A. (editor). 1974. Chromosome Numbers of Flowering Plants. Otto Koeltz Science Publishers, West Germany (reprinted).

Goldblatt, P. 1981a. Cytology and the phylogeny of Leguminosae. Pp. 427–463 *in* R. M. Polhill & P. H. Raven (editors), Advances in Legume Systematics, Part 2. Royal Botanic Gardens, Kew.

——— (editor). 1981b. Index to Plant Chromosome Numbers 1975–1978. Monogr. Syst. Bot. Missouri Bot. Gard. 5: 1–553.

———. 1984. Index to Plant Chromosome Numbers 1979–1981. Monogr. Syst. Bot. Missouri Bot. Gard. 8: 1–427.

———. 1985. Index to Plant Chromosome Numbers 1982–1983. Monogr. Syst. Bot. Missouri Bot. Gard. 13: 1–224.

———. 1988. Index to Plant Chromosome Numbers 1984–1985. Monogr. Syst. Bot. Missouri Bot. Gard. 23: 1–264.

Jafri, S. M. H. 1966. The Flora of Karachi. Book Corporation, Karachi.

Khatoon, S. & S. I. Ali. 1982. Chromosome numbers of some plants of Pakistan. Pakistan J. Bot. 14: 117–129.

——— & ———. 1991. Chromosome numbers in subfamily Papilionoideae (Leguminosae) from Pakistan. Willdenowia 20: 159–165.

Moore, R. J. (editor). 1973. Index to Plant Chromosome Numbers for 1967–1971. Regnum Veg. 90: 1–539.

Quraish, H. B. & S. A. Faruqi. 1970. Genetic system in *Rhyncosia minima* and *R. memnonia* (Leguminosae). Pakistan J. Bot. 2: 65–82.

Srivastav, P. K. & S. N. Raina. 1986. Cytogenetics of *Tephrosia* VI. Meiotic systems in some taxa. Cytologia 51: 359–373.

CHROMOSOME NUMBERS IN COMPOSITAE FROM PAKISTAN[1]

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Abstract

Chromosome numbers of 82 taxa, belonging to 48 genera in ten tribes of the family Compositae, are reported from Pakistan. The chromosome numbers of 13 taxa are reported for the first time, including one new generic count (for *Grantia*) and a new base number ($x = 10$) in *Sonchus*. The new counts are as follows: $n = 6$ for *Launaea tomentella*; $n = 7$ for *Pulicaria gnaphalodes*; $n = 8$ for *Cephalorrhynchus picridiformis*; $n = 9$ for *Artemisia salsolioides*, *Conyza stricta* var. *pinnatifida*, *Grantia aucheri*, *Heteropappus altaicus* var. *canescens*, *Launaea oligocephala*, and *Phagnalon pycnophyllon*; $n = 10$ for *Blumea bovei* and *Sonchus lacnocephalus*; and $n = 14$ for *Scorzonera koelpinioides* and *Scorzonera tortuosissima*. The chromosomal counts for 31 other taxa are new for the flora of Pakistan.

Compositae comprise approximately 20,000 species and about 40% of these have been investigated cytologically (Solbrig, 1977). Very little cytological research has been carried out on the family in Pakistan, where to date chromosome number for only 65 (i.e., ca. 11.0%) of the ca. 604 native species (Ali, 1978) for the family have been counted (Baquar & Askari, 1970; Khatoon & Ali, 1988; Razaq et al., 1988). The present contribution records the chromosome numbers for 82 taxa in 48 genera.

Materials and Methods

Meiotic material consisting of immature capitula, collected mostly in the wild (those which were cultivated are specified in Table 1), was fixed in acetic alcohol (1 : 3) for 24 hr. and stored at −4°C. The slides were prepared by conventional squash technique using aceto- or propionic-carmine. Counts were made from pollen mother cells, except in *Dyssodia tenuiloba*, where both somatic and gametic counts were made.

For mitosis, root tips from germinating seeds were pretreated with 8-hydroxyquinoline for 4 hr., fixed in acetic alcohol (1 : 3) for 1 hr., hydrolysed in 1 N HCl for 6–12 min. and squashed in 1.8% aceto-orcein.

Photomicrographs were taken from temporary mounts, in all cases. Later on slides were made permanent in euparal or Canada balsam.

Observations and Results

A total of 140 chromosomal counts on plants representing 82 taxa belonging to 48 genera of Compositae have been determined. Counts for 13 taxa are reported for the first time, as they were not found to be reported in IPCN (Fedorov, 1974; Goldblatt, 1981, 1984, 1985, 1988; Moore, 1973, 1974; Ornduff, 1967). The classification adopted here follows that of Heywood et al. (1977).

Discussion

Cytologically, Vernonieae are the least known tribe in the family, with fewer than 100 (out of 1450) species so far counted (Mathew & Mathew, 1983). Available cytological data on the genus *Vernonia* (Fedorov, 1974; Jones, 1974; Mathew & Mathew, 1976; Gill, 1978; Keil & Pinkava, 1979; Gupta & Gill, 1979) reveal that species of this genus are based on $x = 9$, 10, and 17. Two of the four species of *Vernonia*, the only genus of Vernonieae in Pakistan (Stewart, 1972), were examined. According to Jones (1977), Old World *Vernonia* have $x = 9$ or 10 and a little polyploidy.

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TABLE 1. Chromosome numbers in Compositae. K.U. = Karachi University; D. G. Khan = town of Dera Ghazi Khan.

Taxon	Chromosome number *n*	Basic number *x*	Voucher
Tribe Eupatorieae			
**Ageratum conyzoides* L. (Fig. 1)	10	10	Sialkot: *Ghafoor 4311*
**Ageratum houstonianum* Mill. (cultivated)	20		K.U. Campus: *Siddiqui 43*
Tribe Vernonieae			
Vernonia cinerascens Sch. Bip.	20	10	K.U. Campus: *Moin. 36*
Vernonia cinerea (L.) Less.	9	9	Kashmir: *T. Ali 112*; Jhelum: *Ghafoor 4278*; Sargodha: *T. Ali 1691*
Tribe Astereae			
Conyza aegyptiaca Ait.	9	9	D. G. Khan: *Ghafoor 3652*
Conyza bonariensis (L.) Cronquist	27		K.U. Campus: *Ahsan 70*; Kathore: *Jahan 75*; Hasan Abdal: *Ghafoor 2270*
**Conyza japonica* (Thunb.) Less.	9		Sargodha: *T. Ali 1655*
***Conyza stricta* Willd. var. *pinnatifida* (D. Don) Kit.	9		Kashmir: *T. Ali 232*
Heteropappus altaicus (Willd.) Novopokr. (Fig. 2)	9	9	Dir: *Ghafoor 2324*; Gilgit: *Omer 2412, 2304, 2305*
***Heteropappus altaicus* (Willd.) Novopokr. var. *canescens* (Nees) Serg. (Fig. 3)	9		Chitral: *Ghafoor 3224*
Heteropappus holohermaphroditus Grierson	9		Quetta: *T. Ali 1414*; D. G. Khan: *Ghafoor 3643*
Myriactis wallichii Less.	18	18	Rawalpindi: *Ghafoor 4119*
Tribe Inuleae			
***Blumea bovei* (DC.) Vatke (Fig. 4)	10	10	Makran: *T. Ali 943*
Blumea lacera DC.	10		K.U. Campus: *Siddiqui 8*
Blumea obliqua (L.) Druce	10		K.U. Campus: *Siddiqui 55, 58*
Gnaphalium luteo-album L.	7	7	Dir: *Ghafoor 2487*; Swat: *Ghafoor 3351*
***Grantia aucheri* Boiss. (Fig. 5)	9	9	Makran: *Omer 2118*
**Inula cuspidata* (DC.) C. B. Clarke	10	10	Hazara: *Omer 2791*
Iphiona grantioides (Boiss.) Anderb. (Fig. 6)	9	9	Makran: *Omer 2052, T. Ali 905*; Safari Park, Karachi: *Siddiqui 62*
Phagnalon niveum Edgew.	9	9	Hazara: *Omer 2262*; D. G. Khan: *Ghafoor 3700*
***Phagnalon pycnophyllon* Rech.f. (Fig. 7)	9		Chitral: *Ghafoor 3157*
Pluchea arguta Boiss. (Fig. 8)	10	10	Makran: *T. Ali 877*
Pluchea indica (L.) Less.	30		Makran: *T. Ali 892*; K.U. Campus: *Jahan 7, 8, 9*
Pluchea lanceolata (DC.) Clarke	10		K.U. Campus: *Jahan 37*
Pulicaria angustifolia DC.	7	7	K.U. Campus: *Siddiqui 40, 49*
***Pulicaria gnaphalodes* (Vent.) Boiss. (Fig. 9)	7		Quetta: *T. Ali 1243*
Pulicaria hookeri Jafri	7		Super Highway, Karachi: *T. Ali 1437*
Tribe Heliantheae			
**Bidens biternata* (Lour.) Merr. & Sherff	36	12	Hazara: *Omer 2233*
Blainvillea acmella (L.) Philipson	17	17	K.U. Campus: *Moin. 41*
Coreopsis atkinsoniana Douglas (cultivated)	12	12	Malir: *Moin. 20*
**Coreopsis lanceolata* L. (cultivated) (Fig. 10)	10	10	K.U. Campus: *Jahan 14, 25*

TABLE 1. Continued.

Taxon	Chromosome number *n*	Basic number *x*	Voucher
**Cosmos bipinnatus* Cav. (cultivated)	12	12	K.U. Campus: *Siddiqui 44*
**Dahlia variabilis* (Willd.) Desf. (cultivated)	32	16	K.U. Campus: *Jahan 15*
Eclipta prostrata (L.) L.	11	11	K.U. Campus: *Siddiqui 9*; Sajawal: *Ahsan 18*; Thatta: *Siddiqui 106, 123*; Khushab: *Ghafoor 3835*; Swat: *Ghafoor 3970*
Flaveria trinervia (Spreng.) C. Mohr	18	18	Kathore: *Jahan 85*
Gaillardia pulchella Fouger (cultivated)	17	17	K.U. Campus: *Siddiqui 24*
**Galinsoga parviflora* Cav.	8	8	Kashmir: *T. Ali 312*; D. G. Khan: *Ghafoor 3650*
**Helianthus annus* L. (cultivated)	17	17	K.U. Campus: *Moin. 9*
**Parthenium hysterophorus* L.	18	18	Gujrat: *Ghafoor 4308*
**Rudbeckia maxima* Nutt. (cultivated)	18	18	K.U. Campus: *Jahan 10*
Tridax procumbens L.	18	9	K.U. Campus: *Siddiqui 26*
**Xanthium strumarium* L.	18	18	K.U. Campus: *Razaq 122*; Ghotki: *Ghafoor 3512*; Kashmir: *T. Ali 198*; Kathore: *Jahan 74*
Zinnia elegans Jacq. (cultivated)	12	12	K.U. Campus: *Moin. 5*
Tribe Tageteae			
**Dyssodia tenuiloba* (DC.) B. L. Robinson (cultivated)	12	12	K.U. Campus: *Ahsan 55*
Dyssodia tenuiloba (Fig. 11)	$2n = 24$		K.U. Campus: *Jahan 51*
**Tagetes minuta* L. (Fig. 12)	24	12	Jhelum: *Ghafoor 3886*; Kashmir: *T. Ali 349*
Tribe Senecioneae			
Hertia intermedia (Boiss.) Kuntze	10	10	Quetta: *T. Ali 1237*
**Senecio analogus* DC.	20	10	Swat: *Ghafoor 3451*
Senecio desfontanei Druce	10		Baltistan: *Omer 2436*; Chitral: *Ghafoor 2551*; Dir: *Ghafoor 2489*
Senecio kraschenninnikovii Schischk.	10		Chitral: *Ghafoor 2741*; Gilgit: *Omer 2520*
Tribe Anthemideae			
Achillea millefolium L.	9	9	Gilgit: *Omer 2326*; Kashmir: *T. Ali 559*
**Anthemis cotula* L.	9	9	K.U. Campus: *Jahan 36*; Kashmir: *T. Ali 511*; Chitral: *Ghafoor 3243, 2976, 2518*
**Artemisia capillaris* Thunb. (Fig. 13)	8	8	Sargodha: *Ghafoor 3801*
**Artemesia persica* Boiss. (Fig. 14)	9	9	Chitral: *Ghafoor 3225, 2571, 2581*
**Artemisa rutaefolia* Spreng. (Fig. 15)	9		Chitral: *Ghafoor 3219*
***Artemisia salsoloides* Willd. (Fig. 16)	9		Gilgit: *Omer 2430*
**Artemisia siversiana* Willd.	9		Chitral: *Ghafoor 3111*
**Handelia trichophylla* (Schrenk) Heimerl	9	9	Chitral: *Ghafoor 3234*
Tanacetum fruticulosum Ledeb. (Fig. 17)	9	9	Gilgit: *Omer 2548*
**Tripleurospermum disciforme* (C. A. Mey.) Sch. Bip.	9	9	Chitral: *Ghafoor 2846*

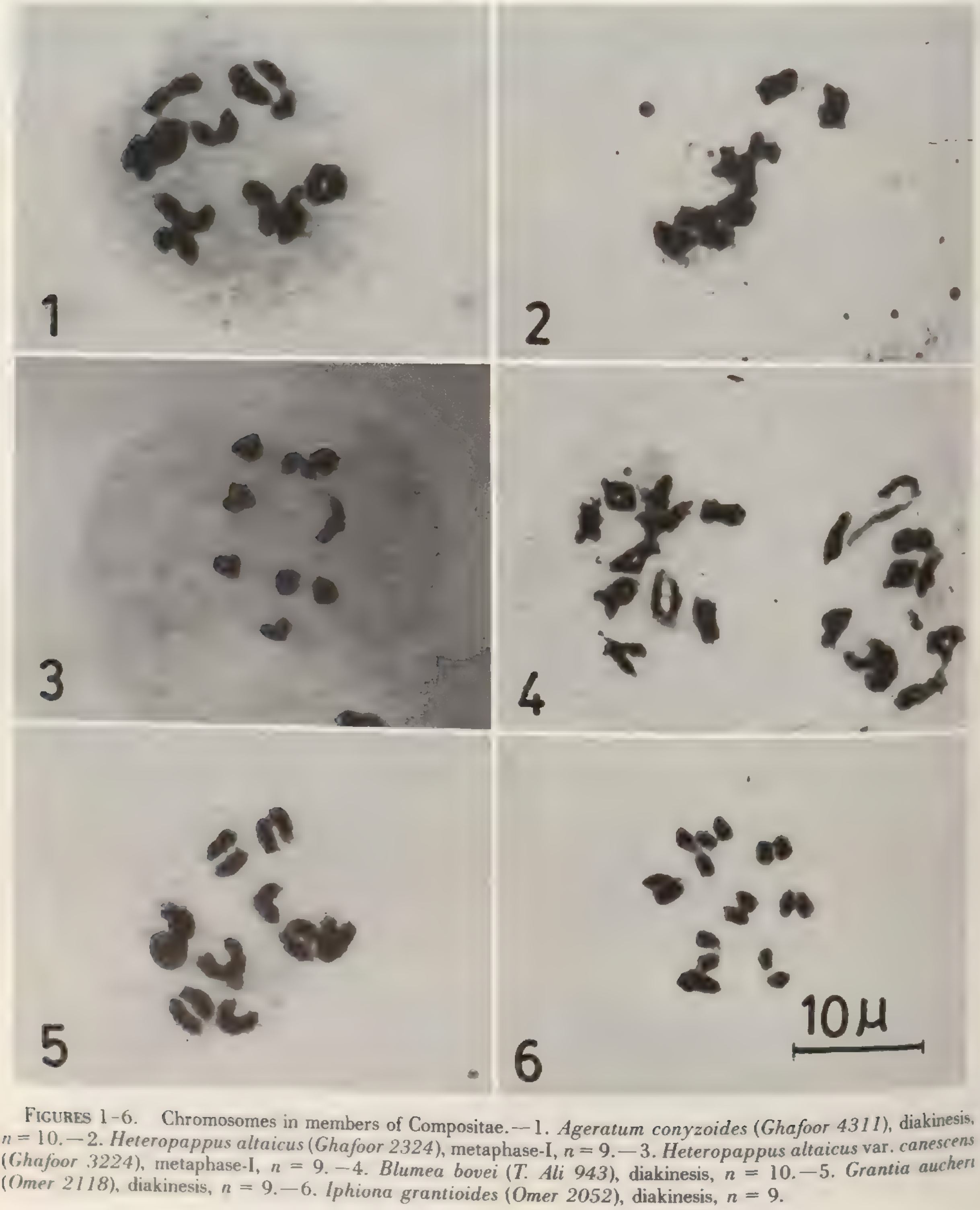
TABLE 1. Continued.

Taxon	Chromosome number *n*	Basic number *x*	Voucher
Tribe Cynareae			
Centaurea cyanus L. (cultivated)	12	12	K.U. Campus: *Jahan 11*
**Oligochaeta ramosa* (Roxb.) Wagenitz	14	14	Darsanochano: *Siddiqui 82*; Makran: *Omer 2090, T. Ali 993*
Tribe Lactuceae			
***Cephalorrhynchus picridiformis* (Boiss.) Tuisl (Fig. 18)	8	9	Quetta: *T. Ali 1394*
**Cichorium intybus* L.	9	9	Thatta: *Siddiqui 105*
**Crepis multicaulis* Ledeb. subsp. *congesta* (Regel) Babc.	5	5	Swat: *Ghafoor 3376*
Crepis sancta (L.) Babc.	5		Chitral: *Ghafoor 2997*
Lactuca dissecta D. Don	8	8	Chitral: *Ghafoor 2951*
**Lactuca serriola* L.	9	9	Attock: *Ghafoor 3888*; Zhob: *T. Ali 1059*
**Launaea capitata* (Spreng.) Dandy	9	9	Makran: *T. Ali 1492*
Launaea nudicaulis (L.) Hook.f.	9		Rawalpindi: *Ghafoor 4175*; Faisalabad; *Ghafoor 4377*; Makran: *T. Ali 708*; Kathore: *Jahan 63*; Sajawal: *Ahsan 15*; Thatta: *Siddiqui 98, 114, 118, 124*
***Launaea oligocephala* (Hausskn. & Bornm. ex Bornm.) Bornm. (Fig. 19)	9		Makran: *T. Ali 953*
**Launaea procumbens* (Roxb.) Ramayya & Rajagopal (Fig. 20)	9		Makran: *Omer 2097, 2040*; Hasilpur: *Ghafoor 3582*
Launaea remotiflora (DC.) Amin ex Rech.f.	9		Safari Park, Karachi: *Siddiqui 71*; K.U. Campus: *Moin. 6*; Kashmir: *T. Ali 271*; Bahlolpur: *Ghafoor 4307*
**Launaea resedifolia* (L.) Kuntze	8	8	Safari Park, Karachi: *Ahsan 39*; Bahawalpur: *Ghafoor 3574*
**Launaea secunda* (C. B. Clarke) Hook.f.	9	9	Chitral: *Ghafoor 2410*
***Launaea tomentella* Rech.f. (Fig. 21)	6	6	Zhob: *T. Ali 1167*
Picris hieracioides L.	5	5	Chitral: *Ghafoor 2583*
***Scorzonera koelpinioides* Rech.f. (Fig. 22)	14	7	Makran: *T. Ali 992*
***Scorzonera tortuosissima* Boiss. (Fig. 23)	14		Makran: *T. Ali 991*
Sonchus asper (L.) Hill	9	9	Kashmir: *T. Ali 578*
***Sonchus lachnocephalus* Rech.f. (Fig. 24)	10	10	Kashmir: *T. Ali 174, 493*
Sonchus oleraceus L.	16	8	K.U. Campus: *Jahan 29*; D. G. Khan: *Ghafoor 3657*
Sonchus wightianus DC.	9	9	Kashmir: *T. Ali 331*; Rawalpindi: *T. Ali 1955*

* Count new to flora of Pakistan.
** Count new to science.

Our counts for *V. cinerascens* ($n = 20$) and *V. cinerea* ($n = 9$) confirm the above statement.

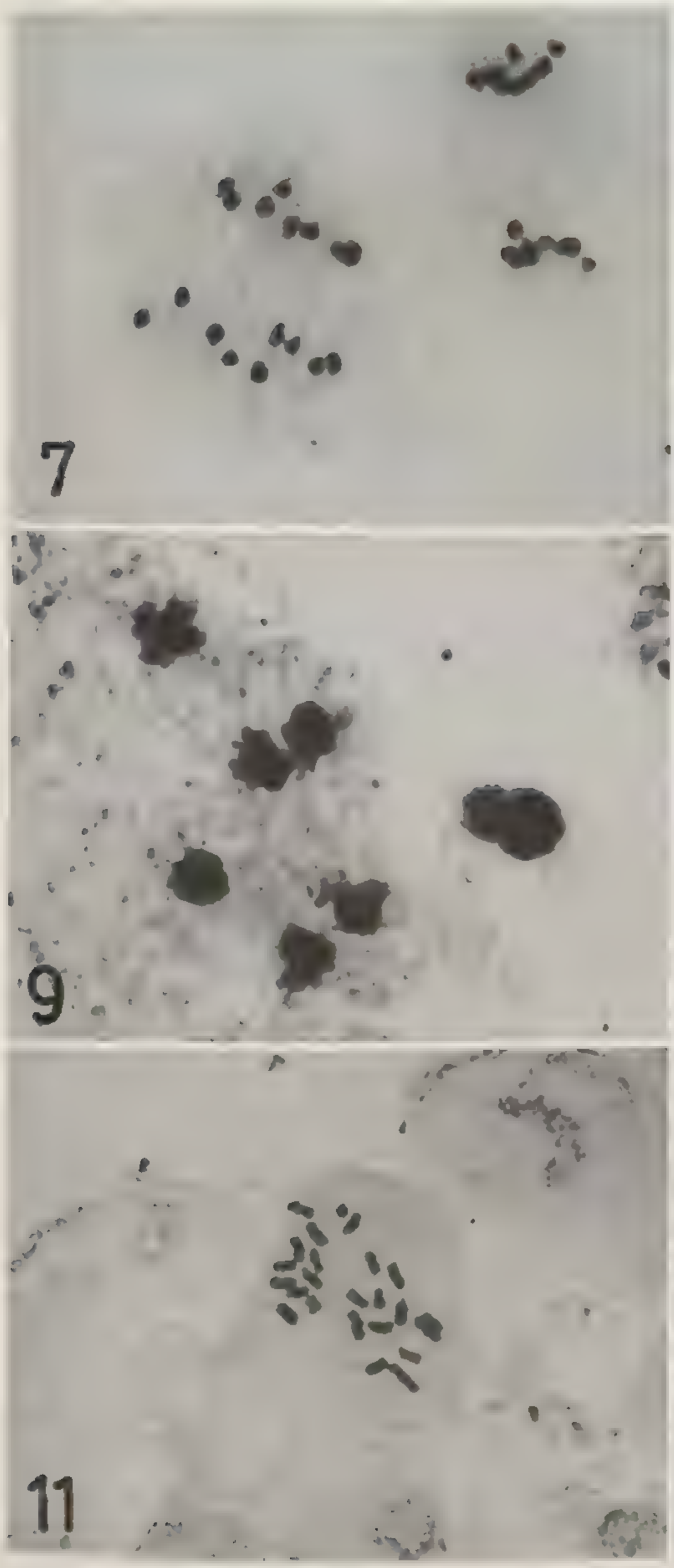
The basic number for various members of Astereae is reported to be $x = 9$ with polyploidy (Raven et al., 1960; Solbrig et al., 1964, 1969; Anderson et al., 1974). Out of eight taxa of Astereae studied, chromosome counts of all the species except *Myriactis wallichii* are based on $x = 9$. All the species of the genus *Myriactis* are reported to have $n = x = 18$.



FIGURES 1–6. Chromosomes in members of Compositae.—1. *Ageratum conyzoides* (*Ghafoor 4311*), diakinesis, $n = 10$.—2. *Heteropappus altaicus* (*Ghafoor 2324*), metaphase-I, $n = 9$.—3. *Heteropappus altaicus* var. *canescens* (*Ghafoor 3224*), metaphase-I, $n = 9$.—4. *Blumea bovei* (*T. Ali 943*), diakinesis, $n = 10$.—5. *Grantia aucheri* (*Omer 2118*), diakinesis, $n = 9$.—6. *Iphiona grantioides* (*Omer 2052*), diakinesis, $n = 9$.

The members of tribe Inuleae exhibit a predominance of the basic numbers $x = 9$ and 10 (Merxmuller et al., 1977). In this tribe, we have examined 15 species in eight genera. Of these, four species (belonging to two genera) are based on $x = 7$, four species (belonging to three genera) on $x = 9$, and seven species (belonging to three genera) on $x = 10$. Our data thus agree with Merxmuller et al.'s conclusion (1977). In Senecioneae, the most frequent basic numbers are multiples of ten (Nordenstam, 1977). Our observations on the chromosome numbers of three species of *Senecio* (Table 1) are based on $x = 10$. The count for *S. kraschenninkovii*, $n = 10$, differs from the previous report of $n = 9$ (Khatoon & Ali, 1988).

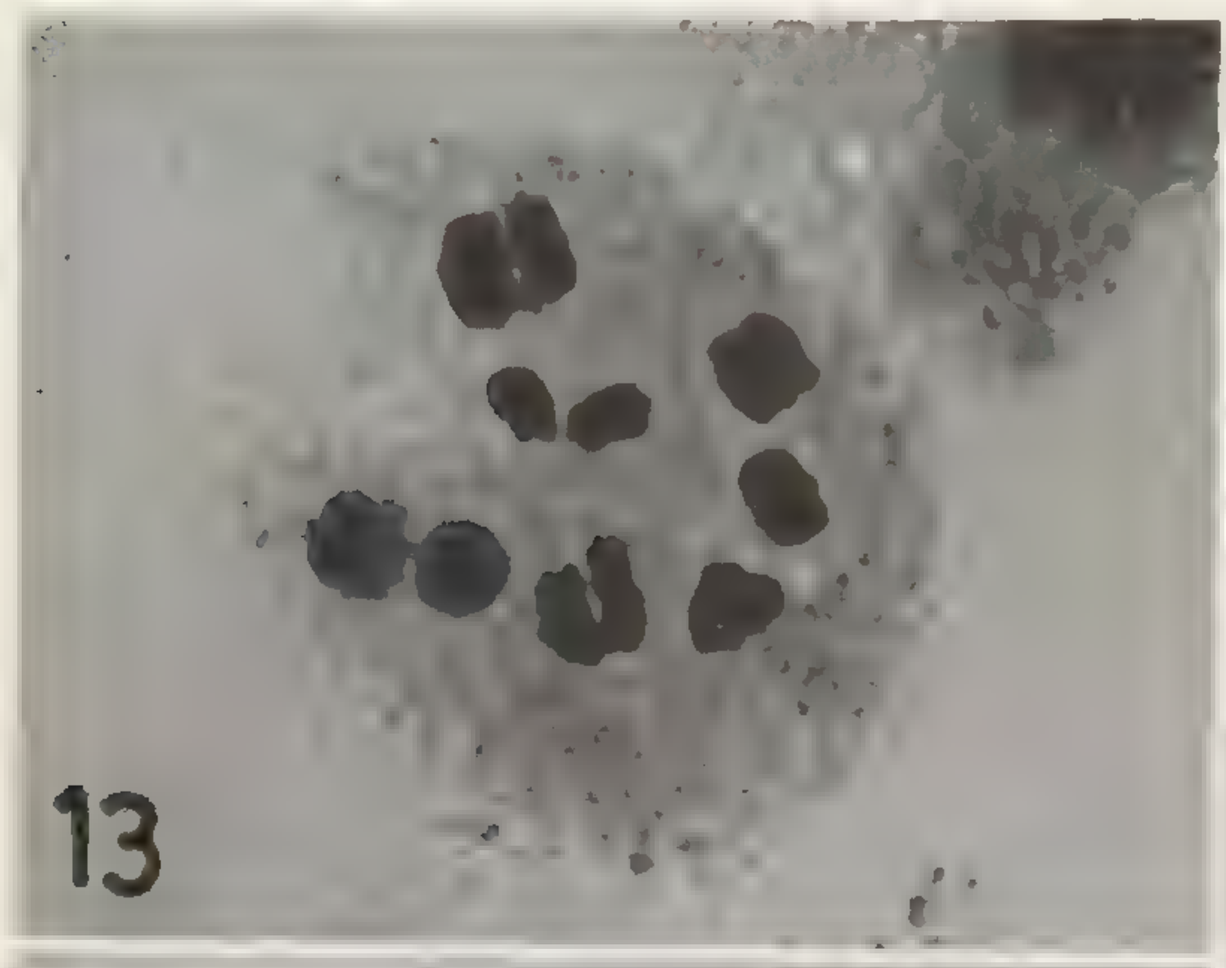
Chromosome counts have been reported for about

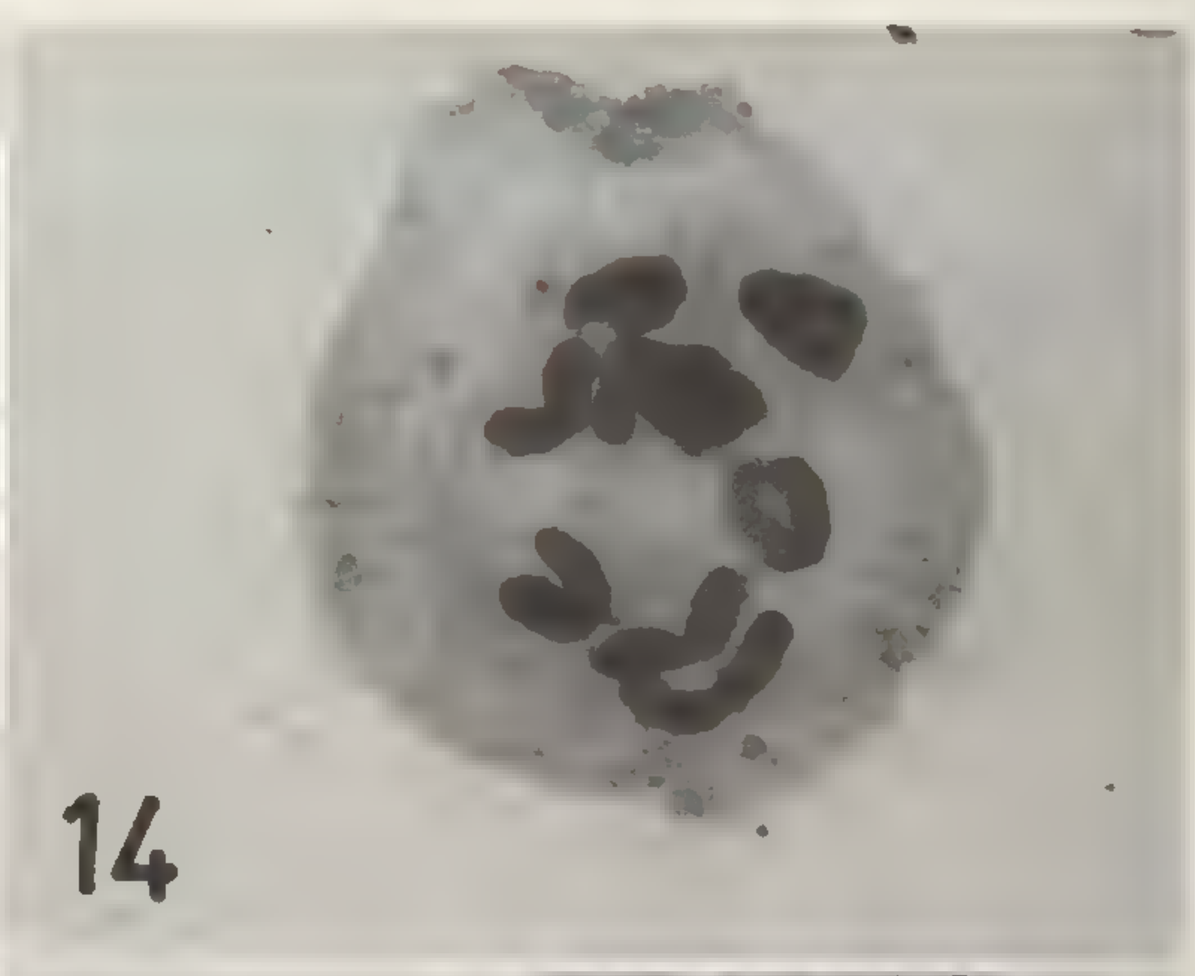


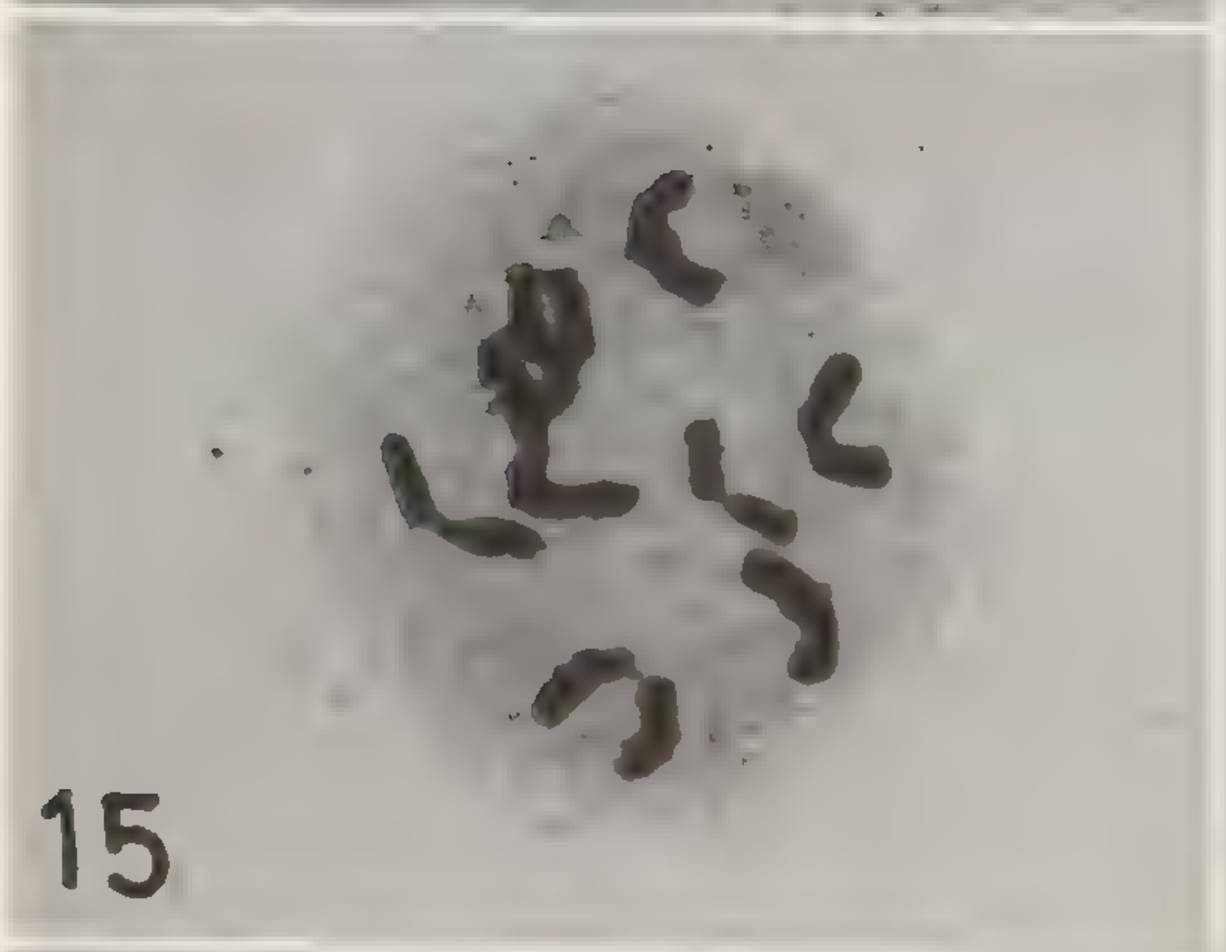
FIGURES 7–12. Chromosomes in members of Compositae.—7. *Phagnalon pycnophyllon* (*Ghafoor 3157*), anaphase-I, $n = 9$.—8. *Pluchea arguta* (*T. Ali 877*), metaphase-I, $n = 10$.—9. *Pulicaria gnaphalodes* (*T. Ali 1243*), diakinesis, $n = 7$.—10. *Coreopsis lanceolata* (*Jahan 14*), diakinesis, $n = 10$.—11. *Dyssodia tenuiloba* (*Ahsan 55*), mitotic metaphase, $2n = 24$.—12. *Tagetes minuta* (*Ghafoor 3886*), diakinesis, $n = 24$.

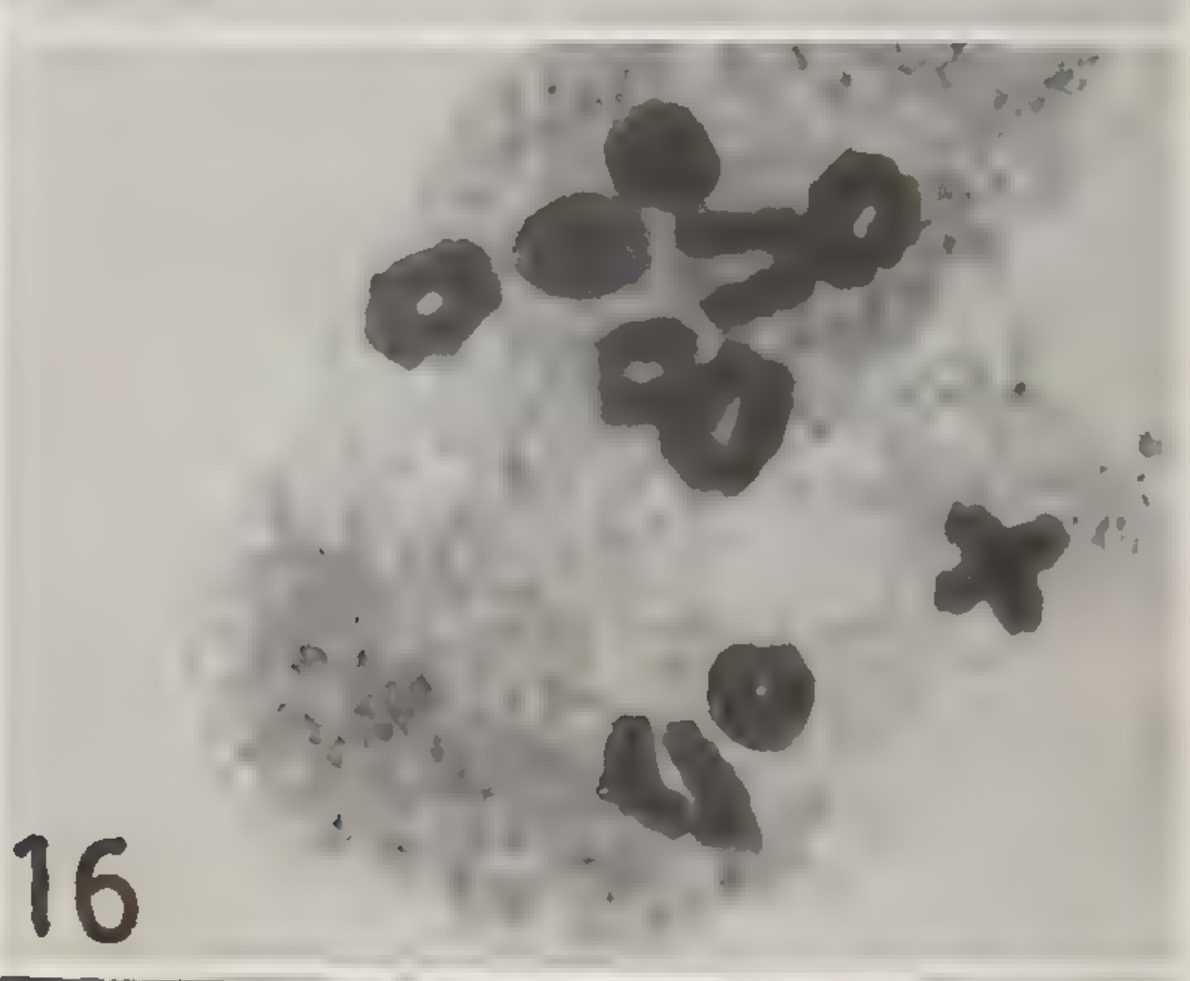
50% of the genera of Anthemideae (Heywood & Humphries, 1977). Ten of the 11 taxa of Anthemideae examined have $n = 9$; *Artemisia capillaris*, however, has $n = 8$ (Fig. 13), a count contrary to the earlier findings ($2n = 18$: Arano, 1965 and $2n = 36$: Peng & Hsu, 1978). The present report may represent aneuploid variation. The most frequent chromosome number in *Artemisia* is $n = 9$ and probably the basic number for the genus was also $x = 9$ (Stahevitch & Wojtas, 1987).

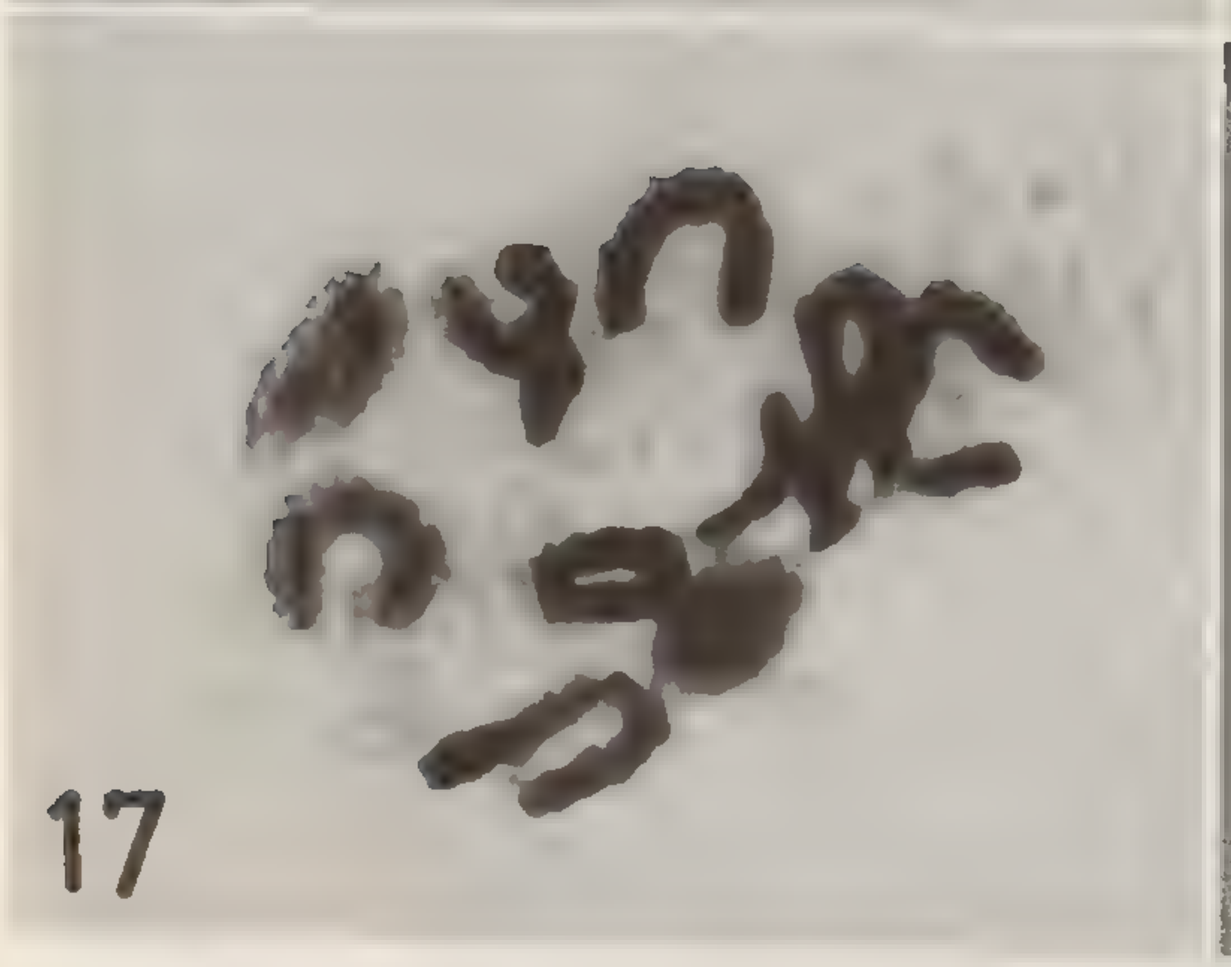
Chromosome numbers for 21 taxa of Lactuceae are reported here. The count for *Cephalorrhynchus picridiformis* ($n = 8$, Fig. 18) does not agree

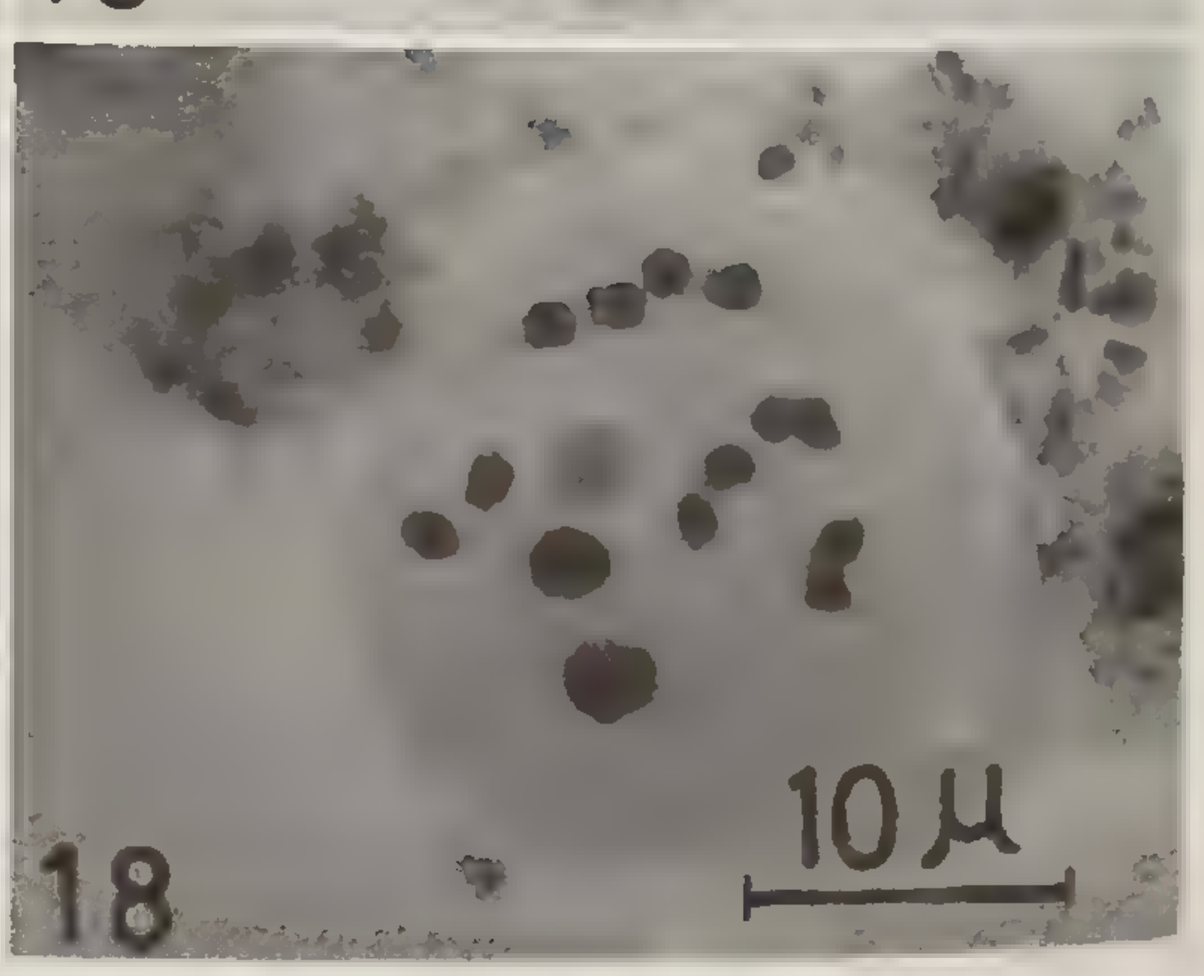






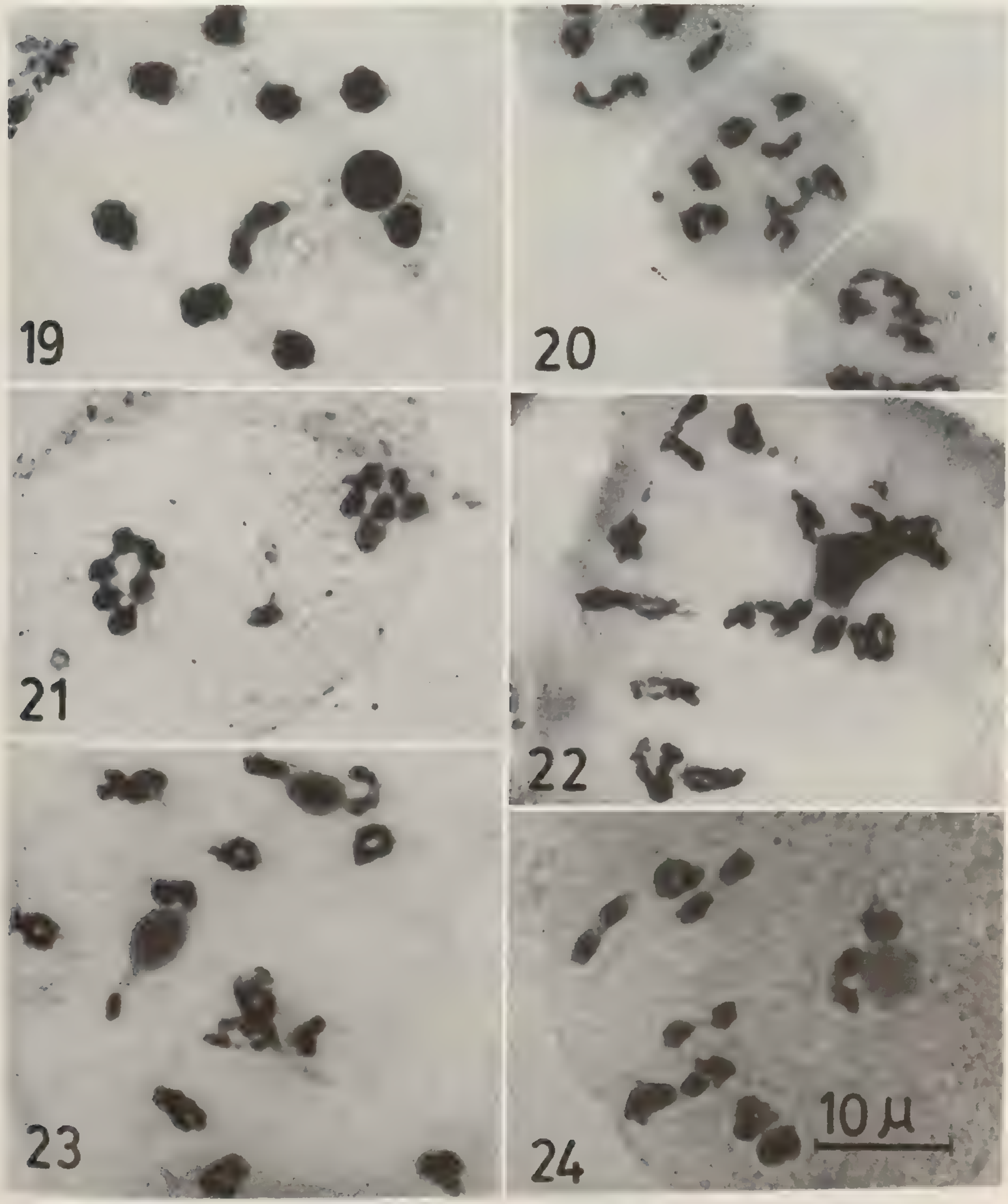






FIGURES 13–18. Chromosomes in members of Compositae. — 13. *Artemisia capillaris* (*Ghafoor 3801*), diakinesis, $n = 8$. —14. *Artemisia persica* (*Ghafoor 3225*), diakinesis, $n = 9$. —15. *Artemisia rutaefolia* (*Ghafoor 3219*), diakinesis, $n = 9$. —16. *Artemisia salsoloides* (*Omer 2430*), diakinesis, $n = 9$. —17. *Tanacetum fruticulosum* (*Omer 2548*), diakinesis, $n = 9$. — 18. *Cephalorrhynchus picridiformis* (*T. Ali 1394*), diakinesis, $n = 8$.

with basic number $x = 9$, proposed by Darlington & Wylie (1955), for this genus. In *Launaea*, $x = 6$, 7, 8, and 9 are reported. However, $n = 6$ has been reported for *L. asplenifolia* Hook. f. by Sarkar et al. (1975). We have observed the same number for *L. tomentella* (Table 1, Fig. 21). For the genus *Sonchus*, $x = 8$ and 9 are reported. Our count of $n = 10$ for *Sonchus lachnocephalus* (Fig. 24) establishes a new basic number ($x = 10$) for the genus. Chromosomally, the Lactuceae are perhaps the best known tribe in the family. Chromosome numbers are known for 87.0% of the genera of the tribe (Tomb, 1977). Stebbins et al. (1953) proposed $x = 9$ as the ancestral base chromosome number for the tribe, on the basis of its frequency of occurrence and presence in genera considered to be primitive. In the present study ten taxa out of 21 examined are found to be based



FIGURES 19–24. Chromosomes in members of Compositae.—19. *Launaea oligocephala* (*T. Ali 953*), diakinesis, $n = 9$.—20. *Launaea procumbens* (*Omer 2097*), diakinesis, $n = 9$.—21. *Launaea tomentella* (*T. Ali 1167*), metaphase-II, $n = 6$.—22. *Scorzonera koelpinioides* (*T. Ali 992*), diakinesis, $n = 14$.—23. *Scorzonera tortuosissima* (*T. Ali 991*), diakinesis, $n = 14$.—24. *Sonchus lachnocephalus* (*T. Ali 174*), diakinesis, $n = 10$.

on $x = 9$, whereas other taxa are based on $x = 5$, 6, 7, and 8.

LITERATURE CITED

ALI, S. I. 1978. The flora of Pakistan: Some general and analytical remarks. Notes Roy. Bot. Gard. Edinburgh 36: 427–439.

ANDERSON, L. C., D. W. KYHOS, T. MOSQUIN, A. M. POWELL & P. H. RAVEN. 1974. Chromosome numbers in Compositae. IX. *Haplopappus* and other Astereae. Amer. J. Bot. 61: 665–671.

ARANO, H. 1965. The karyotypes and the speciations in subfamily Carduoideae (Compositae) of Japan. XVIII. Jap. J. Bot. 19: 31–67.

BAQUAR, S. R. & S. H. A. ASKARI. 1970. Chromosome numbers in some flowering plants of West Pakistan—II. Genét. Ibér. 22: 41–51.

DARLINGTON, C. D. & A. P. WYLIE. 1955. Chromosome Atlas of Flowering Plants. George Allen & Unwin Ltd., London.

FEDOROV, A. A. (editor). 1974. Chromosome Numbers of Flowering Plants. Otto Koeltz Science Publishers, Germany (reprinted).

GILL, B. S. 1978. Chromosome Number Reports LX. Taxon 27: 229–230.

GOLDBLATT, P. (editor). 1981. Index to Plant Chromosome Numbers 1975–1978. Monogr. Syst. Bot. Missouri Bot. Gard. 5: 1–553.

———. 1984. Index to Plant Chromosome Numbers 1979–1981. Monogr. Syst. Bot. Missouri Bot. Gard. 8: 1–427.

———. 1985. Index to Plant Chromosome Numbers 1982–1983. Monogr. Syst. Bot. Missouri Bot. Gard. 13: 1–224.

———. 1988. Index to Plant Chromosome Numbers 1984–1985. Monogr. Syst. Bot. Missouri Bot. Gard. 23: 1–264.

GUPTA, R. C. & B. S. GILL. 1979. Chromosome Number Reports LXIV. Taxon 28: 401–402.

HEYWOOD, V. H. & C. J. HUMPHRIES. 1977. Anthemideae—Systematic review. *In:* V. H. Heywood, J. B. Harborne & B. L. Turner (editors), The Biology and Chemistry of Compositae, Vol. II. Academic Press, London & New York.

———, J. B. HARBORNE & B. L. TURNER (editors). 1977. The Biology and Chemistry of Compositae, Vols. I and II. Academic Press, London & New York.

JONES, S. B. 1974. Vernonieae (Compositae) chromosome numbers. Bull. Torrey Bot. Club 101: 31–34.

———. 1977. Vernonieae—Systematic review. *In:* V. H. Heywood, J. B. Harborne & B. L. Turner (editors), The Biology and Chemistry of Compositae, Vol. I. Academic Press, London & New York.

KEIL, D. J. & D. J. PINKAVA. 1979. Chromosome Number Reports. LXIII. Taxon 28: 271–273.

KHATOON, S. & S. I. ALI. 1988. Chromosome numbers in Compositae from Pakistan. Candollea 43: 455–462.

MATHEW, A. & P. M. MATHEW. 1976. Studies on South Indian Compositae: Cytology of the genus *Vernonia*. Cytologia 41: 401–406.

MATHEW, P. M. & A. MATHEW. 1983. Studies on the South Indian Compositae V. Cytotaxonomic consideration of the tribes Vernonieae and Eupatorieae. Cytologia 48: 679–690.

MERXMULLER, H., P. LIENS & H. ROESSLER. 1977. Inuleae—Systematic review. *In:* V. H. Heywood, J. B. Harborne & B. L. Turner (editors), The Biology and Chemistry of Compositae, Vol. I. Academic Press, London & New York.

MOORE, R. J. (editor). 1973. Index to Plant Chromosome Numbers for 1967–1971. Regnum Vegetabile 90: 1–539.

———. 1974. Index to Plant Chromosome Numbers for 1972. Regnum Vegetabile 91: 1–108.

NORDENSTAM, B. 1977. Senecioneae and Liabeae—Systematic review. *In:* V. H. Heywood, J. B. Harborne & B. L. Turner (editors), The Biology and Chemistry of Compositae, Vol. II. Academic Press, London & New York.

ORNDUFF, R. (editor). 1967. Index to Plant Chromosome Numbers for 1965. Regnum Vegetabile 50: 1–128.

PENG, C.-I. & C.-C. HSU. 1978. Chromosome numbers in Taiwan Compositae. Bot. Bull. Acad. Sin. 19: 53–66.

RAVEN, P. H., O. T. SOLBRIG, D. W. KYHOS & R. SNOW. 1960. Chromosome numbers in Compositae. I. Astereae. Amer. J. Bot. 47: 124–132.

RAZAQ, Z. A., S. KHATOON & S. I. ALI. 1988. A contribution to the chromosome numbers of Compositae from Pakistan. Pakistan J. Bot. 20: 177–189.

SARKAR, A. K., N. DATTA & U. CHATTERJEE. 1975. Chromosome Number Reports XLVIII. Taxon 24: 367–372.

SOLBRIG, O. T. 1977. Chromosomal cytology and evolution in the family Compositae. *In:* V. H. Heywood, J. B. Harborne & B. L. Turner (editors), The Biology and Chemistry of Compositae, Vol. I. Academic Press, London & New York.

———, L. C. ANDERSON, D. W. KYHOS & P. H. RAVEN. 1969. Chromosome numbers in Compositae VII: Astereae III. Amer. J. Bot. 56: 348–353.

———, ———, ———, ——— & L. RUDENBERG. 1964. Chromosome numbers in Compositae V. Astereae II. Amer. J. Bot. 51: 513–519.

STAHEVITCH, A. E. & W. A. WOJTAS. 1987. Chromosome numbers of some North American species of *Artemisia* (Asteraceae). Canad. J. Bot. 66: 672–676.

STEBBINS, G. L., JR., J. A. JENKINS & M. S. WALTERS. 1953. Chromosomes and Phylogeny in the Compositae, Tribe Cichorieae, Univ. Calif. Publ. Bot. 16: 401–430.

STEWART, R. R. 1972. An annotated catalogue of the vascular plants of West Pakistan and Kashmir. *In:* E. Nasir & S. I. Ali (editors), Flora of Pakistan. Karachi.

TOMB, A. S. 1977. Lactuceae—Systematic review. *In:* V. H. Heywood, J. B. Harborne & B. L. Turner (editors), The Biology and Chemistry of Compositae, Vol. II. Academic Press, London & New York.

BOOK REVIEWS

B. P. M. Hyland & T. Whiffin. 1993. Australian Tropical Rain Forest Trees. Accompanying Leaf Atlas by D. C. Christophel and B. P. M. Hyland, to be ordered from CSIRO Information Services, P.O. Box 89, East Melbourne, Victoria 3002, Australia (Fax: 613-419-0459). ISBN 0-643-05403-0 (set). Price: $A195 in Australia, or U.S. $195 outside, plus shipping and handling ($A20 within Australia, U.S. $25 outside Australia).

The *Australian Tropical Rain Forest Trees*, an interactive identification system, consists of several components. The main part is the computer-based key, which is supplied in two versions, MS-DOS and MacIntosh. These disks are accompanied by three printed volumes. Volume 1 contains instructions for loading and using the computer keys, an explanation of characters used in the keys, and several lists: a list of genera with family name used in the key, a species list by code number, a species list by family, a species list by genus, a list of common names, and a glossary. Volume 2 provides a list of all included species, arranged alphabetically by family and genus, with a short description and discussion of additional features and distribution. Volume 3 is a leaf atlas, which presents excellent photographs of the leaf venation of all included species.

The main attraction of this identification system is the computer key. The key consists of nine separate files, which include lists of bark, leaf, flower, fruit, and seedling characters, families treated, list of characters used, and a list of the remaining characters. For identification one simply indicates which of the listed character states are present on the specimen to be identified. The computer eliminates from consideration all taxa in which the characters are lacking and in this way the pool of possible species becomes smaller. At any time one can check the list of remaining species and determine which characters have been scored as present. This type of key has several advantages over the traditional keys found in floras and revisions. One advantage is that characters can be scored in any sequence. Any character may be used as a starting point. The absence of a key to families and the presence in the key of easy to observe vegetative features (such as leaf position, presence of domatia) make the key very user-friendly. The brief descriptions and additional features listed in Volume 2 enable the user to confirm or narrow down identifications in cases where following the computer key resulted in a few possible identifications. It is also possible to limit the pool of species by including only species from a particular area (the area covered by the flora is divided into three regions), or only species from a particular family. Another option is to list all the features of a particular species, a sort of identification in reverse.

This entire identification package is developed for anyone wishing to identify Australian rain forest trees, not solely botanists. I have used the key on several herbarium specimens without using bark or seedling features. I found the key a pleasure to use. Frequently the key leaves one with a handful of possible identifications, but in that case the leaf atlas and the additional notes listed in Volume 2 are very helpful. Also, when left with a few possible names, it is relatively easy to compare the specimens with herbarium material. The entire process of identifying is quick and easy. However, even with this key, identification becomes difficult when the specimens are poor. As pointed out in the instructions, not all features are of equal value. For instance, leaf margins entire or toothed is a more reliable character than length/width ratio of the leaves. Occasionally it is difficult to choose between character states; for instance, do Lauraceae have one perianth whorl or two similar perianth whorls? Because each choice seems equally possible, the authors scored Lauraceae as having both character states; such safeguards make seemingly difficult choices easy to make. Still, because of the enormous amount of information included in the key, one can expect some minor problems, in spite of the extensive testing to which the key was subjected. If errors are found, they will be relatively easy to correct, and updated versions of the key can be sent to the users.

With a price of U.S. $200, this identification system will be too expensive for most individuals and will largely be bought by institutional libraries. Upon request these institutional users can receive permission to place up to ten copies of the key on PCs of staff members. Time will tell if this is ad-

equate; having the key available only on a PC in the library is clearly not practical. Very few institutions are networked to the degree that one copy is accessible to all connected users, although that seems the preferred solution.

The three hard-copy volumes are attractively produced and seem free of errors. I only wish that author names had been added to the species descriptions and diagnoses in Volume 2. This volume will probably be the most intensively used of the three, and having the author names included here would have been very practical.

I strongly recommend this publication to anyone interested in Australian rain forest trees. Its key and the photographs of leaf venation are outstanding features, and I think this publication offers the nonbotanist a realistic possibility of identifying Australian rain forest trees. My only question to the authors: When can we expect a treatment for the rest of the world?—Henk van der Werff, *Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166-0299, U.S.A.*

Flora of Australia, Vol. 50, Oceanic Islands 2. 1993. Australian Government Publishing Service, GPO Box 84, Canberra, ACT 2601. xxvi + 606 pp. ISBN 0-644-14446-7 (paperbound version), $A44.95.

The fourteenth chronological volume published in the *Flora of Australia* series is somewhat of a departure from its predecessors. An editorial decision early in the project's planning resulted in the exclusion of the several groups of islands surrounding the Australian continent from the flora proper, and the compilation of separate accounts for the floras of these lands. The present volume details the vegetation and flora of a diverse group of islands, which includes Cocos Island, Christmas Island, Cartier Island, and the Ashmore Reef National Nature Reserve off Australia's northwestern coast, the Coral Sea Islands Territory to the east and northeast, Macquarie Island, which is southwest of New Zealand, and Heard and McDonald Islands far to the southwest of the Australian continent. The companion volume 49 will contain florulas for Lord Howe and Norfolk Islands, the remaining islands.

Volume 50 includes approximately 500 species of vascular plants in 113 families. It contains one new species, one new combination, two lectotypifications, and one neotypification, which are summarized in a short appendix. The organization of the main text is unusual. Each island group receives a separate summary of climate, geography (including a simple map), geology, vegetation, history (including botanical), use by wildlife, and bibliography, as well as a key to families and a useful table of species present, including an indication of endemics and introduced taxa. These occupy only the first 62 pages of the book. The background summaries are brief, but relatively complete, although given the small sizes of the land masses involved and relative simplicity of the vegetation, some mapping of the major vegetational types for at least the larger islands should have been included.

The bulk of the volume contains a combined treatment of the taxa within each family that occur on any of the islands. This includes keys, detailed descriptions at all taxonomic levels, synonymy, distributional summaries, miscellaneous notes on each taxon, and a citation of representative specimens. Each family also has a separate citation of pertinent taxonomic literature. This unique organization results in a volume that is taxonomically cohesive, with the species easily located in the text, while simultaneously allowing for convenient access to information specific to a particular island. A table summarizing the species shared by different islands and the percentage of each island's flora also present on the continent would be useful once the remaining islands have been treated in the companion volume 49.

Eleven contributors wrote the text for volume 50. As has been the case with previous volumes in the *Flora of Australia* series, the information in the present volume is wonderfully detailed and easy to use. The indented keys are clear and well constructed. The descriptions are of parallel construction within each group and use clear terminology. There are a number of abbreviations and contractions throughout the text, which are summarized at the end of the volume, and which do not detract from its ease of use. The descriptions of vegetation and taxa are beautifully supplemented with a number of graphics. There are 42 black-and-white plates illustrating about 100 species, the work of three talented artists. A beautiful color cover and frontispiece by Diana Boyer illustrates *Pandanus tectorius*. There are also 55 photographs (by 11 photographers) of vegetation types and species that are uniformly excellent in clarity and reproduction.

The Flora Editorial Committee and the contributors to this book are to be congratulated on the completion of yet another volume of the *Flora of Australia*, which continues to set new standards for elegance and detail in the presentation of floristic data. I am eager to see the companion volume that will complete the island florulas, as well as future volumes on the continent's flora.—George Yatskievych, *Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166-0299, U.S.A.*

ANNALS OF THE MISSOURI BOTANICAL GARDEN: CHECKLIST FOR AUTHORS

1. General Instructions

- ☐ Text is in English or Spanish on numbered pages.
- ☐ Manuscript is typed on one side of nonglossy 8½ × 11 in. paper.
- ☐ At least 1 in. is left as margin all around, except on the first page, which has 3 in. left blank at the top.
- ☐ Three copies of double- or triple-spaced printed manuscript, including abstract, notes, legends, tables, specimen lists, Literature Cited, and footnotes, are enclosed.
- ☐ Manuscript is also submitted on MS-DOS 3½ in. diskette, as WordPerfect® [preferable] file.
- ☐ Right-hand margin is not justified, and words are not broken there.
- ☐ Words to be set in italics are underlined instead of italicized. Boldface or other special typefaces are not used. [Editor will add printer's marks for these.] Common Latin words or phrases are not italicized (e.g., et al., i.e., sensu, etc.).
- ☐ Only names at the rank of genus and below are italicized.
- ☐ Correct accents, umlauts, and other diacritical marks have been included.
- ☐ All figures and tables are cited in the text.
- ☐ Photocopies of the figures are included with each copy of the manuscript.

2. Style

- ☐ Recent issue of the *Annals* is used as a model.
- ☐ *Chicago Manual of Style*, latest edition, is used as a reference.

3. First Page

- ☐ Footnotes are typed as double-spaced paragraphs on the first page. The first footnote contains acknowledgments, including information on granting agencies, herbaria that loaned specimens, and the name of the artist. The second footnote is the author's address. Addresses for additional authors are each separate footnotes. No other footnotes occur, except in tables, where unavoidable.

4. Abstract

- ☐ A one-paragraph abstract precedes text. Papers in Spanish have an English abstract in addition to a Spanish resumen.
- ☐ The abstract is concise (1 paragraph) and includes brief statements about the paper's intent, materials and methods, results, and significance of findings.

5. Tables

- ☐ Tables are neat, double-spaced, and easily understood rather than long and complex.
- ☐ Tables do not contain vertical or horizontal lines. [Editor and/or printer will add them as needed.]
- ☐ Captions are typed double-spaced as paragraphs at the tops of the tables.
- ☐ Each table starts on a separate sheet, double-spaced.

6. Abbreviations

- ☐ Periods are used after all abbreviations (which are minimized) except metric measures, compass directions, and herbarium designations.
- ☐ When dates are given as part of collection information, three-letter month abbreviations are used, except for months with four letters, which are spelled out in full.
- ☐ States are not abbreviated, and cities are spelled out. [St. is acceptable.]
- ☐ Periodicals are abbreviated according to *B-P-H* (*Botanico-Periodicum-Huntianum*) and to *B-P-H/S* (*Botanico-Periodicum-Huntianum/Supplementum*).
- ☐ Authors' names are abbreviated according to *Authors of Plant Names* or spelled out in full.
- ☐ Book titles are abbreviated according to *Taxonomic Literature*, edition 2, but with initial letters capitalized. Book titles are spelled out in the Literature Cited.
- ☐ Authors' names in major taxonomic citations, such as the formal citation at the head of a taxonomic treatment, are spelled out.
- ☐ Herbaria are abbreviated according to *Index Herbariorum*, edition 8.

7. Taxonomic Treatment

- ☐ One paragraph per basionym is used as follows: *Taxon* author, literature citation, type citation, e.g., *Pleurothyrium amplifolium* (Mez) Rohwer, Mitt. Inst. Allg. Bot. Hamburg 20: 43. 1986. *Nectandra amplifolia* Mez, Arbeiten Königl. Bot. Gart. Breslau 1: 131. 1892. TYPE: Brazil. Rio de Janeiro Alto Macahé, *Glaziou 17731* (holotype, B; isotypes, B, G, K, NY, P). Figure 11.
- ☐ Lectotype designations are included together with an indication of where they were designated, the year, and the author. This reference is listed in the Literature Cited. If the author of the paper submitted is making the lectotypification, the phrase "selected here" is used.
- ☐ Exclamation points are not used for specimens examined. Types not seen are indicated as such (e.g., MO, US not seen).
- ☐ A brief Latin diagnosis for each new taxon is provided rather than a complete Latin description.
- ☐ When relevant, nomina nuda, misapplied names and superfluous names are included in the discussion following the description, but are not part of the formal synonymy.

8. Specimens Examined

- ☐ If many specimens were examined, those cited in the text are limited to one collection per geographical area
- ☐ Long lists of specimens examined are placed at the end of the paper, following the Literature Cited. They

are arranged alphabetically by collector, followed by collection number, followed by the number of the taxon in the text.

- ☐ Specimens are cited in the text as follows: *Additional specimens examined* (or *Selected specimens examined* or *Paratypes*). MEXICO. Oaxaca: Sierra San Pedro Nolesco, Talea, 3 Feb. 1987 (fl), *Jergensen 865* (BM, G, K, US). [Dates and reproductive status are optional.] Countries are run together in the same paragraph, e.g., COUNTRY A. Major political division: . . . COUNTRY B. Major political division: . . .

9. Vouchers and Genetic Sequences

- ☐ If paper presents original data, it includes citation of vouchers. [Depending on the type of paper, reference to the original wild source may also be required.]
- ☐ Herbarium vouchers state the collector and number, herbarium in which the voucher is located, and a clear annotation that the material represents the voucher for the study in question.
- ☐ Genetic sequences have been banked, and accession numbers are provided.
- ☐ Author accepts responsibility for establishing the accuracy of information provided.

10. Keys

- ☐ Keys are clear and have been checked carefully for consistency with the descriptions.

11. Literature Cited

- ☐ The Literature Cited contains all references cited in the text.
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- ☐ Spelling of author(s) name(s) and years of publication have been double-checked.
- ☐ All entries have been verified against original sources, especially journal titles, accents, diacritical marks, and spelling in languages other than English.
- ☐ Periodicals are listed as follows: author's last name, initial(s). Year. Full title of article. Journal abbreviated as in *B-P-H/S*. Volume: pages. No parenthetical part numbers after volume numbers are given unless each part is paginated separately.
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- ☐ Books appear as follows: author's last name, initial(s). Year. Full Unabbreviated Title (edited by Editor), 3rd ed., Vol. 2. Publisher, City of Publication.
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- ☐ Scale bars appear on illustrations, photographs, and maps.
- ☐ Magnifications/reductions are not indicated in captions.
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